

Origin, evolution and systematics of the dwarf Acanthoceratid *Protacanthoceras* Spath, 1923 (Cretaceous Ammonoidea)



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Contents

Synopsis	65
Introduction	66
Evolutionary origins	66
Dimorphism	67
Localities	67
Stratigraphy	68
Systematic descriptions	68
Family Acanthoceratidae Hyatt	68
Genus <i>Protacanthoceras</i> Spath	68
<i>Protacanthoceras tuberculatum</i> Thomel	71
<i>Protacanthoceras tuberculatum tuberculatum</i> Thomel	71
<i>Protacanthoceras tuberculatum</i> Thomel <i>mite</i> subsp. nov.	74
<i>Protacanthoceras tuberculatum</i> Thomel <i>devonense</i> subsp. nov.	76
<i>Protacanthoceras tuberculatum</i> Thomel <i>cyclopeum</i> subsp. nov.	80
<i>Protacanthoceras arkelli</i> sp. nov.	82
<i>Protacanthoceras arkelli arkelli</i> subsp. nov.	84
<i>Protacanthoceras arkelli verrucosum</i> subsp. nov.	86
<i>Protacanthoceras tegulicium</i> sp. nov.	88
<i>Protacanthoceras asgeirri</i> sp. nov.	90
<i>Protacanthoceras bunburianum</i> (Sharpe)	91
<i>Protacanthoceras proteus</i> sp. nov.	95
<i>Protacanthoceras proteus proteus</i> subsp. nov.	95
<i>Protacanthoceras proteus baylissi</i> subsp. nov.	96
<i>Protacanthoceras imperatoris</i> sp. nov.	97
Other species previously referred to <i>Protacanthoceras</i>	99
' <i>Acanthoceras</i> ' <i>cuspidum</i> Stephenson	99
' <i>Acanthoceras</i> ' aff. <i>cuspidum</i> Stephenson	100
<i>Ammonites tropicus</i> Stoliczka	101
<i>Ammonites triserialis</i> J. de C. Sowerby	101
<i>Protacanthoceras</i> sp. nov. (?) of Matsumoto, Saito & Fukada	102
Discussion: Evolutionary trends	102
Acknowledgements	104
References	104
Index	106

Synopsis

Protacanthoceras Spath, 1923 is a dwarf acanthoceratid of middle and late Cenomanian age. Individuals are adult at diameters of 15–50 mm and some populations show apparent size dimorphism indicating that the genus is genuinely diminutive, not the microconch of some larger acanthoceratid.

The earliest species, *P. tuberculatum* Thomel, is a paedomorphic derivative of contemporary *Acanthoceras rhotomagense* (Brongniart); later species diverged considerably from the basic long-ranging ribbed,

square-whorled prototype. Decline in ornament led to *P. tuberculatum mite* subsp. nov., whence was derived *P. arkelli* sp. nov. in the late Middle Cenomanian, and the early Upper Cenomanian *P. asgeirri* sp. nov. In the early Upper Cenomanian *P. arkelli* gave rise to a further paedomorphic offshoot which led to the aberrant *P. tegulicium* sp. nov. During middle Upper Cenomanian time there arose three rectangular-whorled forms, a small robust subspecies, *P. tuberculatum devonense* subsp. nov., *P. tuberculatum cyclopeum* subsp. nov. (the largest form of the genus), and the compressed *P. bunburianum* (Sharpe). *P. tuberculatum devonense* gave rise to a round-whorled form which lost its tubercles, *P. proteus* sp. nov., with two subspecies *P. p. proteus* and *P. p. baylissi* subsp. nov.

The late Cenomanian *Protacanthoceras* assemblage exhibits in miniature the features of the early growth stages of several latest Cenomanian and early Turonian genera.

Protacanthoceras is best known in England and France but a further species, *P. imperatoris* sp. nov., is described from Madagascar.

Other species have been referred to the genus incorrectly.

Introduction

Protacanthoceras Spath, 1923 is among the most variably interpreted of Cenomanian acanthoceratid genera. Originally described, on the basis of misconceptions about its stratigraphic range, as an intermediate between *Calycoceras* Hyatt, 1900 of the Mantelliceratinae and *Acanthoceras* Neumayr, 1875 of the Acanthoceratinae, the generic name has been, and still is, applied to diverse convergent acanthoceratids linked only by their closely trituberculate peripheries. The genus in fact comprises genuine dwarfs, adult at diameters of 15–50 mm, and, unlike some other dwarf taxa which subsequent work has shown to be no more than microconchs of normal-sized ammonites, it appears to be dimorphic within these size limits. *Protacanthoceras* at its origin is thus an exception to the widely quoted phenomenon of progressive size increase amongst ammonites (Cope's Rule, e.g. Stanley 1973). As discussed below, evolution within the genus demonstrates both size increase and size decrease, whilst both at its origin and subsequently paedomorphosis produced abrupt species transformations. Furthermore, the late Cenomanian array of *Protacanthoceras* reproduces in miniature several latest Cenomanian and early Turonian genera.

Evolutionary origins

Spath's original view (1923 : 144) that *Protacanthoceras* preceded *Acanthoceras*, with *P. triseriale* (J. de C. Sowerby) as the passage form closest to *Calycoceras*, was probably based on his ideas on the sequence of Cenomanian ammonites which derived from faunas collected by T. F. Grimsdale and others from the Chalk Basement Bed in south Dorset and the Cenomanian Limestone of Devon. In 1926 he noted that *Hyphoplites* occurred with '*Protacanthoceras*' of the '*hippocastanum*' group in this area, without realising that these condensed units contained mixed faunas (cf. Kennedy 1970). In fact work on the expanded chalk sequences of south-east England shows quite clearly that *Acanthoceras* precedes *Protacanthoceras* and that its origins in all probability lie in robustly ornamented *Acompsoceras* of the group of *sarthense* (Guéranger) or *landesii* Cobban (= *Paracompsoceras* Cobban, 1971).

Thomel (1972 : 99, text-fig. 3) suggested that *Protacanthoceras* evolved from early *Pseudocalyoceras* Thomel, 1969 and placed both in the Mantelliceratinae. Again stratigraphic evidence renders this view untenable. The earliest known *Pseudocalyoceras* appears in the Upper Cenomanian, while *Protacanthoceras* appears low in the Middle Cenomanian. Juvenile *Pseudocalyoceras* are so different in their ribbing and tuberculation (Cobban & Scott 1972 : pl. 13, figs 11–25) that no close relationship can be inferred and the similar clavate ventral ornament of adults is merely homoeomorphy (Figs 8, 9). Thomel's view (1972 : 99) that *Protacanthoceras* might be the microconch of *Pseudocalyoceras* cannot be supported. The two genera show none of the features in common which are seen in dimorphic pairs and have quite different stratigraphic and geographic distributions.

Morphological evidence points very clearly to *Acanthoceras* of the *rhotomagense* (Brongniart) group as the immediate ancestor of *Protacanthoceras*. Immature specimens of the earliest species, *P. tuberculatum* Thomel, show such striking similarities to juveniles of strongly-ribbed variants such as *A. rhotomagense sussexiense* (Mantell) and *confusum* (Guéranger) (Figs 11, 12) that affinity

cannot be doubted. Indeed, only the parallel sides and more markedly clavate outer ventrolateral and siphonal tubercles allow the inner whorls of *tuberculatum* to be distinguished, although the adult ornament of *Protacanthoceras* (e.g. Fig. 8) is immediately diagnostic, as is the change from alternately long and short ribs of the juvenile *Acanthoceras rhotomagense* to the wholly long ribs of middle and later growth.

Whereas adult sutures of *Acanthoceras* differ at first sight from adult sutures of *Protacanthoceras*, they are on the same essential plan, as is indicated by the resemblance between the sutures of juvenile *Acanthoceras* and adult *Protacanthoceras* (Fig. 1), whilst the very earliest ornamented stage of *A. rhotomagense* and *P. tuberculatum*, with round whorls and sparse, band-like tuberculate ribs, are identical.

No intermediates are known between *Acanthoceras* of the *rhotomagense* group and *Protacanthoceras tuberculatum* and the generic transformation does not appear to have involved progressive size decrease. Sudden pedomorphosis seems to be the most probable explanation of the evolution from a species group that is adult between 150–200 mm to one whose macroconchs are adult at 30–37 mm.

The smallest adult *Acanthoceras* is that described as *A. basseae* by Kennedy & Hancock (1970 : pl. 47, figs 2a–c) from the Middle Cenomanian, but even here the holotype shows a change to adult *Acanthoceras* ornament with all the ribs extending to the umbilicus, whilst its general proportions and whorl section are sufficiently different from *P. tuberculatum* to preclude it from any direct relationship.

We have suggested (Wright & Kennedy in Juignet *et al.* 1973 : 26) that certain *Thomelites* might be the macroconchs of *Protacanthoceras*. It now appears that *Protacanthoceras* is itself dimorphic and that the 'Protacanthoceras' species we there referred to are in fact small *Thomelites*, and indeed microconchs. Differences between *Thomelites* and *Protacanthoceras* (Figs 6, 8) are clarified in the taxonomic part of the paper.

Dimorphism

Dimorphism, although well documented in many groups of Jurassic and some Cretaceous ammonites (Makowski 1962; Callomon 1963; Le Hégerat 1973; Kennedy & Cobban 1976), has not been generally recognized amongst normally-coiled Upper Cretaceous ammonites. *Protacanthoceras* (and probably other acanthoceratids—see, for instance, Berthou *et al.* 1976, Cooper 1978) appears to show dimorphism that is largely a matter of bimodal size distribution, with microconchs only slightly smaller, around 70% of the size of the macroconch, and without lappets, rostra or other apertural modifications. This is in marked contrast to Jurassic groups, where the size difference is often two- to four-fold. Figs 24–33, 36–45 show presumed dimorphic pairs of typical *Protacanthoceras* species. Our samples are generally too small to quantify ratios of the members of pairs with any precision, but samples of *P. tuberculatum* and *P. bunburianum* suggest a ratio of one to one. This size dimorphism, though strongly suggested, is not proved; the spread of size in presumed macroconchs and microconchs within a species may be greater than the gap between the two. However, virtually all the material has been collected from condensed phosphatic beds; the real constituents of any momentary population and exact contemporaneity of individuals cannot be established and it is probable that there was some variation in size during the time represented by each condensed bed.

Localities

To save repetition, full details are given here of localities frequently mentioned in the text (National Grid references in brackets):

Askerswell, Dorset (SY 529923), temporary section 300 m S of church (Kennedy 1970: 644).

Bindon Slips, Devon (SY 272886), *in situ* and slipped masses at top of cliff west of where coastguard path dips over cliff edge.

Chardstock, Devon (ST 316044), old quarries on eastern side of Storridge Hill (Kennedy 1970: 651).

Chilfrome Lane, Maiden Newton, Dorset (SY 593979), old quarry (Kennedy 1970: 634).

Durdle Cove, Dorset (SX 805803), natural exposures west of Durdle Door.

- Evershot, Dorset (ST 578050), old quarry behind Rock Cottages (Kennedy 1970: 632).
 Furley, Devon (SY 208999), disused quarries (Kennedy 1970: 654).
 Hooken Beach, Devon (SY 222878), fallen blocks on beach.
 Hooken Cliff, Devon (SY 220880), slipped masses.
 Horn Hill, Beaminster, Dorset (ST 470032), old quarry on Horn Hill, east of road (Kennedy 1970: 640).
 Humble Point, Devon (SY 307889), fallen blocks on beach (Kennedy 1970: 658).
 Lulworth Cove, Dorset (SX 825800), natural exposures at back of Cove.
 Man-of-War Cove, Dorset (SY 815810), natural exposures at back of Cove.
 Osmington, Dorset (SY 726819), blocks on beach and in landslips inland, west of Osmington Mills.
 Ringstead Quarry, Dorset (SY 747818), disused quarry on west side of road between Upton and Ringstead (Wright *in* Arkell 1947: 211).
 Shapwick Grange, Devon (SY 313918), working lime-pit close to farm.
 Snowdon Hill, Chard, Somerset (ST 313089), old quarry on south side of road A30 west of town (Kennedy 1970: 648).
 Toller Porcorum, Dorset (SY 567982), disused quarry (Kennedy 1970: 637).
 White Hart Sandpit, Wilmington, Devon (SY 208999), working sandpit at western end of village, opposite White Hart Inn.
 White Nothe, Dorset (SY 772806), cliff exposures and slipped masses below Holworth House.
 Whitlands, Pinhay Bay, Devon (SY 313905), slipped masses in undercliff.

Stratigraphy

The basic succession of Cenomanian ammonite faunas in the expanded chalk sequences of south-east England (Kennedy 1969, 1971) provides the framework against which the evolution of *Protacanthoceras* has been worked out. In this region, however, the genus is rare and only the sequence of the main *Protacanthoceras tuberculatum*-*P. bunburianum* rootstock of the genus can be traced. In contrast, the condensed phosphatic Basement Beds of the Chalk of south-west England (Kennedy 1970) yield many more ammonites, and provided most of our *Protacanthoceras* material. These Basement Beds can be precisely correlated with the Chalk sequence and allow dating of the remaining species. It must, however, be stressed that these Basement Beds are in some cases equivalent to many metres to the Chalk sequence and species and subspecies of slightly differing ages are present in a single bed. Here evolutionary relationships are established on the basis of either morphology or relative degrees of mineralization and abrasion.

Systematic descriptions

Superfamily ACANTHOCERATAEAE Grossouvre, 1894

Family ACANTHOCERATIDAE Grossouvre, 1894

Subfamily ACANTHOCERATINAE Grossouvre, 1894

Genus *PROTACANTHOCERAS* Spath, 1923

TYPE SPECIES. *Ammonites bunburianus* Sharpe (1853 : 25; pl. 9, figs 3a-c), by the original designation of Spath (1923 : 144).

DIAGNOSIS. Small. Adult at diameters of 15–50 mm. Moderately involute, compressed to depressed, flat-sided or round-whorled, bearing primary and intercalated ribs, typically with prominent umbilical and inner¹ ventrolateral tubercles and closely spaced clavate outer ventrolateral and siphonal tubercles; tuberculation declines at the end of the body chamber and the ribs become broad and flat. Dimorphic, microconchs generally less densely and more strongly ribbed than macroconchs, although both show essentially similar styles of ornament. In a few species some or all tuberculation except for the umbilical is suppressed during part or all of ontogeny. Suture simple, with broad bifid L and smaller bifid U₂. E/L larger, bifid; L/U₂ small, simple. Auxiliaries may be pseudoceratitic.

¹ The *Treatise* terms 'upper' and 'lower', as applied to ventrolateral tubercles, are illogical. 'Inner' and 'outer' are therefore used instead.

DISCUSSION. *Protacanthoceras* was introduced by Spath in 1923 without diagnosis. He included *P. triseriale* (J. de C. Sowerby), *P. compressum* (Jukes-Brown) and *P. hippocastanum* (J. de C. Sowerby) in the genus at that time and regarded it as intermediate between *Calycoceras* and *Acanthoceras*. Subsequently Collignon (1937) included a series of Madagascan and Algerian ammonite species in the genus and later (*in Roman* 1938 : 443) gave the first diagnosis of the genus: 'Acanthocératidés comprimés, aux côtes plus ou moins flexueuses, parfois droites, de section ogivale, à trois rangées de tubercles ventraux serrées l'une contre l'autre. Cloison du type general d'*Acanthoceras*. Les caractères distinctifs sont la compression de l'Ammonite et la présence de trois rangées de tubercles ventraux serrées, l'une contre l'autre'. This diagnosis was widely accepted and diverse Cenomanian ammonites with three rows of closely spaced clavate ventral tubercles were referred to *Protacanthoceras*, most of them much larger than the type species, including forms up to 150–200 mm diameter.

In 1951 Wright & Wright pointed out that the genus was in fact a genuine dwarf and that most of the species referred to the genus by other authors belonged elsewhere. Thomel (1969) proposed the genus *Pseudocalycoceras* to accommodate the *harpax* group, with their diagnostic rursiradiate ribs, whilst we (*in Juignet et al.* 1973) proposed *Thomelites* to accommodate various other species which closely resembled *Protacanthoceras* but grew to much larger sizes. At that time we suggested that some *Protacanthoceras* might be microconch *Thomelites*; our subsequent work indicated that these specimens are indeed microconchs, but are *Thomelites*.

The characteristic ornament of the end of the body chamber, appearing at small sizes, is the easiest way of separating *Protacanthoceras* from other genera, but when juveniles only are available problems may arise.

Acanthoceras Neumayr, 1875 reaches a large size (commonly in excess of 400 mm) when adult. Early whorls may be separated from *Protacanthoceras* in that most individuals are much less strongly ribbed at the same size as adult *Protacanthoceras* and do not show the same closely-spaced ventrolateral tubercles (Fig. 11A). The sutures of juvenile *Acanthoceras* are always more complex than those of mature *Protacanthoceras* of similar size. Flat ventral ribbing without tubercles is never seen in juvenile *Acanthoceras*. The earliest *Protacanthoceras*, *P. tuberculatum* (Fig. 8), is at

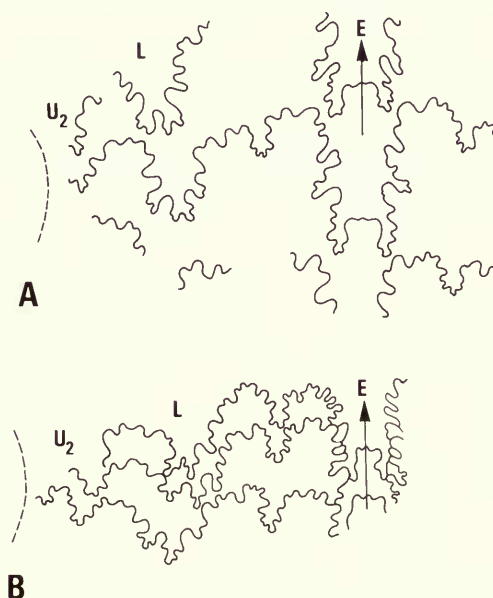


Fig. 1 Sutures of adult Middle Cenomanian *Protacanthoceras* and juvenile *Acanthoceras* compared. 1A, *Acanthoceras rhotomagense* (Brongniart). P. Juignet coll. no. 1-159, from the phosphatic *costatus* Zone fauna at the base of the Craie de Théligny of Sarthe, France, $\times 4$. 1B, *Protacanthoceras tuberculatum tuberculatum* Thomel from the *acutus* Zone fauna of the Chalk Basement Bed, Snowdon Hill, Chard, Somerset. OUM K4437, $\times 4$.

first glance indistinguishable from some contemporary *Acanthoceras rhotomagense* variants in all but size, suture and grouping of ventral tubercles (Figs 11, 12).

Pseudocalycoceras Thomel, 1969 reaches a moderate size, up to 100 mm. Most species bear dense, rounded ribs, which become markedly rursiradiate during middle and later growth (Fig. 9), a feature never seen in *Protacanthoceras*. The juveniles of *P. dentonense* (Moreman), as figured by Cobban & Scott (1972 : pl. 13, figs 11–23), do not develop the strong clavate ventral tuberculation which characterizes the adult and which led previous authors to refer species such as *Pseudocalycoceras harpax* (Stoliczka) and its allies to *Protacanthoceras*.

Thomelites Wright & Kennedy, 1973 reaches a large size. All species retain siphonal tubercles to a much larger size than *Protacanthoceras* (Fig. 6). Compressed forms may lose their inner ventrolateral tubercles at an early stage, leaving a flat venter with the siphonal tubercle weaker than the outer ventrolaterals. Robust forms develop massive inner ventrolateral spinose or subspinose tubercles on primary ribs, with two or three intercalated ribs lacking such a tubercle, a style of ornament never seen in *Protacanthoceras*. The suture of *Thomelites* (Fig. 23E, p. 81) is deeply incised and subdivided compared with that of *Protacanthoceras*.

Metoicoceras Hyatt, 1903 reaches a large size. Juveniles of most species lack siphonal tubercles at all stages in ontogeny (e.g. Cobban 1953 : pl. 6, figs 1–11), have a tiny shallow umbilicus with an outward-sloping umbilical shoulder and have a suture which tends toward development of entire, pseudoceratitic auxiliaries on the suspensive lobe (Fig. 23C, p. 81). Two species, *M. praecox* Haas and *M. latoventer* Stephenson, develop siphonal tubercles when young; in neither are they closely-spaced and clavate as in *Protacanthoceras*.

The largest known individuals of *Neocardioceras* Spath, 1926 are somewhat larger than adult *Protacanthoceras*. All *Neocardioceras* bear dense, flexuous sharp ribs, all or virtually all of which are long. The coiling is very evolute; whilst the inner ventrolateral tubercles disappear early in ontogeny, the outer are bullate rather than clavate and those of the siphonal row are small and separated from the ventrolateral row by a smooth band. Adults never develop the late body chamber ornament of *Protacanthoceras*.

Nigericeras Schneegans, 1943 reaches a large size. Juveniles (Fig. 10) of *Nigericeras costatum* Barber (1957 : pl. 10, figs 3a–b) bear band-like ribs similar to those on the phragmocone of *P. asgeirri* (Figs 20–21) and the earliest ornamented growth stages of other *Protacanthoceras* (Figs 24, 28). The great difference in size and distinctive ornament of later stages in both genera preclude confusion.

The type species of the interesting genus *Quitmaniceras* Powell, 1963, *Q. reaseri* Powell (1963 : 313; pl. 32, figs 5, 13; text-fig. 2A–B), is densely and flexuously ribbed with a carinate venter and is thus readily distinguished from all *Protacanthoceras*. *Q. brandi* Powell (1963 : 314; pl. 32, figs 6, 8, 11, 12, 14–16), however, closely resembles late *Protacanthoceras* like *P. bunburianum* but has flexuous ribs and a crenulate siphonal keel rather than a row of discrete tubercles. The sutures of the two genera are both rather simple.

Calycoceras Hyatt, 1900 species are moderately to very large and have rounded whorls and only faintly clavate tubercles which may be lost at an early stage (Fig. 7). Juvenile *C. (Conlinoceras)* Cobban & Scott, 1972 closely resembles *Protacanthoceras* of the *tuberculatum* group, especially subspecies *mite*, but the ventral tuberculation is never so clavate nor so closely spaced as in *Protacanthoceras*, and *Conlinoceras* lose their tubercles and develop a rounded venter as size increases. Juveniles of *C. (Newboldiceras)* Thomel, 1972 are usually densely ribbed and never show such strong close-spaced ventral tuberculation as *Protacanthoceras*. The sutures of *Calycoceras* (Fig. 23B, p. 81) include broad, sometimes intricately divided lobes and saddles, whilst the auxiliary elements on the suspensive lobe are far more divided than in *Protacanthoceras*.

OCCURRENCE. *Protacanthoceras* first appears as a great rarity at the top of the *Turrilites costatus* Zone, in the lower third of the Middle Cenomanian. It ranges to the middle of the Upper Cenomanian, the higher parts of the *Calycoceras naviculare* Zone.

The genus is best known from southern England (Middle and Upper Cenomanian of Devon and Dorset; Middle Cenomanian of Somerset, Wiltshire, Kent and Sussex). There are also records from the Middle Cenomanian of Rouen, Normandy (Kennedy & Hancock 1970), Sarthe

(specimens in the collection of P. Juignet, Caen, and the Faculté des Sciences, Rennes) and Provence (Thomel 1972) in France. Collignon noted a species from Tihhrert, Algerian Sahara (1965 : 12); the description however suggests it may be a *Pseudocalycoceras*. *Ammonites tropicus* Stoliczka, previously suggested as a possible Indian representative of *Protacanthoceras* (Kennedy 1971 : 97), is a *Thomelites* (p. 101); the Madagascan specimens referred to *tropicum* are indeed *Protacanthoceras* and are described below (p. 97) as a new species, *Protacanthoceras imperatoris*, of presumed Upper Cenomanian age. '*Acanthoceras*' *cuspidum* Stephenson (p. 99) is shown to be a juvenile *Acanthoceras* or *Dunveganoceras* and a homoeomorph of *Protacanthoceras*. Matsumoto, Saito & Fukada's (1957 : 39; pl. 14, fig. 3) specimen from Japan is too juvenile for certain determination.

Protacanthoceras is generally very rare; in the Middle Cenomanian *Turrilites costatus* and *acutus* Zones it accounts for less than 0.1% of the ammonite fauna. It is a little commoner in the succeeding *jukesbrownei* and basal *naviculare* Zones, but still forms less than 1% of the fauna. In the high *naviculare* Zone faunas of south Devon, however, it is one of the commonest ammonites. In England most specimens come from the condensed phosphatic Basement Beds of the south-west. This reflects merely the selective preservation of small ammonites in this facies and the fact that our collections from these fossil concentrates are far larger than from the standard Chalk facies.

Only eight specimens definitely referable to the genus are known from outside the United Kingdom.

Protacanthoceras tuberculatum Thomel

1972 *Protacanthoceras tuberculatum* Thomel: 101; pl. 32, figs 9–12.

HOLOTYPE. G. Thomel colln no. 17523, a macroconch, from the Upper Cenomanian of Peille, Alpes-Maritimes, France, by monotypy. The associated fauna suggests that the specimen is from a horizon equivalent to the lower part of the English *naviculare* Zone.

DIAGNOSIS. A species of *Protacanthoceras* with generally robust ornament of 12–19 alternately long and short ribs per whorl (although feebly ornamented subspecies are known) and a quadrate, angular costal whorl section. Long ribs bear strong umbilical bullae and all ribs bear blunt to spinose inner ventrolateral tubercles and well-developed clavate outer ventrolateral and siphonal tubercles.

Protacanthoceras tuberculatum tuberculatum Thomel

(Figs 1B, 2, 8, 14–17)

1969 *Protacanthoceras* sp. Kennedy : 469, 485, 487, 500, 538 and 542.

1970 *Protacanthoceras* sp. Kennedy : 633, 634, 638, 641, 653 and 654.

1970 *Protacanthoceras* sp. Kennedy & Hancock: pl. 97, figs 4a–b.

1971 *Protacanthoceras* sp. a; Kennedy : 644.

1972 *Protacanthoceras tuberculatum* Thomel : 101; pl. 32, figs 9–12.

HOLOTYPE. G. Thomel colln no. 17523, as above.

MATERIAL. Numerous specimens, including the following (National Grid references in brackets). From the *Turrilites costatus* Zone fauna of the Chalk Basement Bed, Worbarrow Bay, Dorset (SY 865804): BM(NH) C82006. From the *Turrilites acutus* Zone fauna of the Chalk Basement Bed: BM(NH) C9424 from Maiden Newton, Dorset (precise locality unknown); BM(NH) C9563 and OUM K4432 from Evershot; OUM K4436–7 from Toller Porcorum; OUM K4483 from Chilfrome Lane, Maiden Newton; BM(NH) C72911 and OUM K4470 from Horn Hill, Beaminster; OUM K4436–39 from Snowdon Hill. From the Chalk Basement Bed blocks in the landslips west of Osmington, Dorset (*Acanthoceras jukesbrownei* Zone): BM(NH) C72919–24, C81904–9. Of like age and from the same horizon at Ringstead, Dorset are BM(NH) C81910–5; from Chaldon, Dorset (precise locality unknown) is GSM 36927; from Holworth House, White Nothe, Dorset (SY 773807) is BM(NH) C72939; C70956 is also from White Nothe, as is, presumably, a specimen labelled 'White Nose Cape', C55867; C81916 is from Durdle Cove;

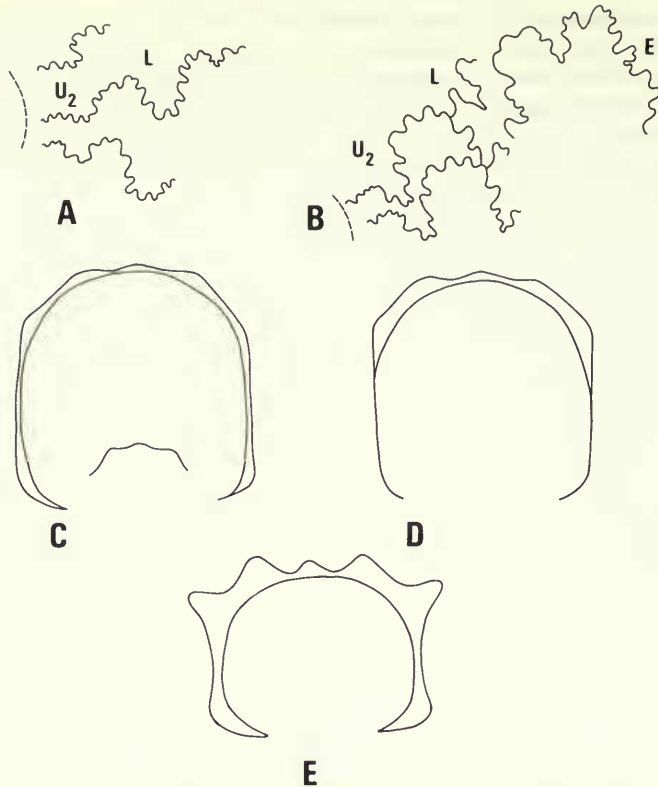


Fig. 2 *Protacanthoceras tuberculatum tuberculatum* Thomel. 2A, juvenile sutures of OUM K4429, $\times 4$. 2B, mature sutures of OUM K4436, $\times 4$. 2C, whorl section of BM(NH) C81905 at aperture, $\times 2$. 2D, whorl section of body chamber of BM(NH) C81906 through an intercalated rib, $\times 2$. 2E, whorl section of BM(NH) C81904 at back of body chamber, $\times 2$.

C81917–9 are from Man-of-War Cove and a specimen in J. M. Hancock's collection is from Furley.

C81920 and C81922 are from the top of the local equivalent of Division B of the Cenomanian Limestone at the White Hart Sandpit, Wilmington and of Middle Cenomanian age.

Calycoceras naviculare Zone: OUM K4426–31 are from the Chalk Basement Bed at Askerswell, Dorset. BM(NH) C81921 and C81923 are from the remanié phosphatic fauna at the base of Division C of the Cenomanian Limestone near Whitlands, Pinhay Bay and from a higher level in the *naviculare* Zone.

Specimens from the Chalk facies of south-east England include OUM K4481 from the *costatus* Zone (Band 6f) below Beachy Head, near Eastbourne, Sussex (TQ 593955); OUM K4482 from the *acutus* Zone (Band 6), Bluebell Hill, Burham, Kent (TQ 735618) and OUM K4480 from the *jukesbrownei* Zone at Newington's Pit, Glynde, Sussex (TQ 430922).

DIAGNOSIS. A subspecies of *Protacanthoceras tuberculatum* characterized by strong ornament, 17–19 alternately long and short straight ribs per whorl, the long ribs bearing variable but generally strong umbilical bullae. All ribs bear subequal, conical to spinose inner ventrolateral tubercles and strong, equal, clavate outer ventrolateral and siphonal tubercles borne on strong transverse ribs. Body chamber modifications include decline in strength of flank ribs and all tubercles, with strengthening and projection of ventrolateral and ventral ribs into a marked chevron.

DESCRIPTION. The coiling is moderately involute on the phragmocone, tending to be rather more evolute on the adult whorl, the umbilical seam of the body chamber being markedly eccentric

(Figs 16b, 17b). The umbilicus is of variable breadth, 20–25% of the total diameter in most specimens, tending towards the lesser figure in juveniles and the greater in adults, as indicated in the table of measurements below.

The umbilicus is of moderate depth, with a rounded umbilical wall and a crenulate umbilical seam to accommodate the ribs on the previous whorl. The umbilical shoulder is sharply rounded. The intercostal section displays flattened, subparallel flanks and a broadly rounded venter, the greatest breadth being around mid-flank. It is always depressed, breadth to height ratios varying greatly, from 1.41 to 1.04. The costal section is also generally depressed, the breadth to height ratio varying from 1.34 to 1.00. The whorl section becomes relatively less depressed towards the adult aperture, in association with a decline in ornament. The greatest breadth is at the inner ventrolateral tubercle, when present.

Ornament is variably developed, tending to become stronger as the whorl breadth to height ratio ($Wb : Wh$) increases.

The smallest individual we have seen (OUM K4429; Fig. 28) shows the early stages of ornament at a diameter of 4 mm, with sparse, broad ribs bearing relatively massive, conical inner ventrolateral tubercles and clavate outer ventrolateral and siphonal tubercles. Our other material shows the ornament from 12 mm onwards. On the phragmocone there are 17–19 ribs per whorl. Nine variably-developed umbilical bullae are borne at the umbilical shoulder; from these arise one or two strong to weak, broad, rounded, radial to prorsiradiate straight ribs, whilst shorter intercalated ribs arise low on the flanks, one or rarely two such ribs being intercalated between the bullate ribs or groups of ribs.

Virtually all ribs bear spinose to conical inner ventrolateral tubercles which are of equal development on both primary and intercalated ribs. Only rarely does a short rib lack such a tubercle, although the strength of tubercles varies greatly. From the inner ventrolateral tubercles the ribs strengthen and broaden, passing somewhat forwards across the ventrolateral shoulder to well-marked clavate outer ventrolateral tubercles, between which a lower, broader rib passes straight across the venter, bearing a clavate siphonal tubercle of similar size and shape to the outer ventrolateral. There is wide variation in the relative dominance of ribbing over tuberculation in our material, some specimens showing very delicate flank ribs and bullae, although all show strong ventrolateral ornament (compare Fig. 17a–b and Fig. 15a–b).

Modification of body chamber ornament associated with maturity is similar in both macroconchs, maturing between 30 and 37 mm, and microconchs, maturing between 20 to 27 mm. Ornament on the earliest parts of the body chamber resembles that of the phragmocone. Towards the aperture, however, the whorl section becomes less depressed, the umbilical bullae and flank ribs decline markedly (Figs 16b, 17b) whilst ventrolateral and ventral ribbing becomes stronger and more crowded and is projected into a distinctive tongue-shaped fold; the ventrolateral tubercles decline markedly (Fig. 15a).

The suture (Fig. 2A–B) is of basic *Protacanthoceras* type, with a deep E, broad bifid L and smaller bifid U_2 . E/L is large and bifid, L/ U_2 smaller, but also bifid. There is a series of small rather simple auxiliaries.

DIMENSIONS. Percentage figures in brackets.

	D	Wb	Wh	Wb : Wh	U
OUM K4432	25.3 (100)	11.4 (45)	11.4 (45)	1.0	5.0 (20)
BM(NH) C81924	34.5 (100)	15.0 (43)	15.2 (44)	0.99	7.9 (23)
BM(NH) C81904 at c	—	16.0	11.9	1.34	—
Ic	—	14.4	10.2	1.41	—
BM(NH) C81908 at c	22 (100)	11.9 (54)	10.2 (46)	1.16	4.5 (20)
Ic	22 (100)	10.2 (46)	8.7 (39)	1.17	—
BM(NH) C74796 at c	27.3 (100)	14.5 (53)	12.8 (47)	1.13	6.8 (25)
Ic	27.3 (100)	12.2 (45)	11.7 (42)	1.04	—
OUM K4427	37.2 (100)	17.2 (46)	15.4 (41)	1.11	8.9 (24)
OUM K4436	25.0 (100)	11.5 (46)	11.3 (45)	1.01	6.7 (26.8)
BM(NH) C9424	24.3 (100)	11.3 (46)	10.5 (43)	1.07	4.6 (19)

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb : Wh</i>	<i>U</i>
BM(NH) C9563	28.0 (100)	13.1 (47)	12.5 (45)	1.04	7.5 (27)
BM(NH) C72923	20.5 (100)	—	8.9 (43)	—	4.1 (20)
BM(NH) C72924	22.5 (100)	12.9 (57)	10.5 (46)	1.22	5.4 (24)
BM(NH) C72911	27.5 (100)	12.9 (46)	12.5 (45)	1.03	5.6 (20)

DISCUSSION. The holotype of *P. tuberculatum tuberculatum* is crushed and distorted, but nevertheless recognizable as either a juvenile or the phragmocone of a macroconch. Our uncrushed material shows the very distinctive ornament and proportions of the subspecies which of all *Protacanthoceras* most closely resembles the ancestral *Acanthoceras*. Indeed, juveniles pose difficulties of separation, but the following features of *P. t. tuberculatum* are distinctive: flattened whorls, strong, equal, clavate ventrolateral tubercles and, when preserved, the adult body chamber modifications.

The subspecies is readily distinguishable from most other *Protacanthoceras*, most closely resembling *P. tuberculatum cyclopeum* subsp. nov. (p. 80). That subspecies, which comes from a higher stratigraphic horizon than that of the acme of *P. t. tuberculatum*, is larger, has much blunter, coarser ornament throughout and inner ventrolateral tubercles which are strongly developed on long ribs and weakly developed on short ribs, in contrast to the far more uniform development of *P. t. tuberculatum*.

Macroconchs and microconchs of *P. tuberculatum devonense* subsp. nov. (p. 76) are significantly smaller than their equivalents in *P. t. tuberculatum*, much more coarsely ribbed and tuberculate (generally around 12 ribs per whorl rather than 17–19), and have umbilical bullae which are stronger than the inner ventrolateral, the reverse of the situation in *P. t. tuberculatum*. Many specimens of *P. t. devonense* show irregularities in ventral ribbing and a highly distinctive rounding of the venter which is transitional towards *Protacanthoceras proteus* sp. nov. (p. 95).

P. t. tuberculatum differs from *P. tuberculatum mite* subsp. nov. (below) in having strong rather than weak tubercles, broad straight rather than delicate flexuous or sometimes effaced flank ribs and stronger and far more clavate ventral tuberculation.

OCCURRENCE. *P. tuberculatum tuberculatum* is the most widespread *Protacanthoceras* in the Chalk Basement Beds of south-west England, first appearing as a great rarity high in the *Turrilites costatus* Zone, commonest in the *Acanthoceras jukesbrownei* Zone of the area and also occurring in the basal *naviculare* Zone Basement Bed fauna at Askerswell (Dorset). A few specimens are known from Division C of the Cenomanian Limestone of the coast; the two specimens from Wilmington are from a local equivalent of Division B of the Cenomanian Limestone and are of Middle Cenomanian age. The species is also known from the chalk facies of south-east England, being recorded from *costatus*, *acutus* and *jukesbrownei* Zones as a great rarity (Kennedy 1969 : 469, 487, 500, 538 and 542, as *Protacanthoceras* spp.). A *Protacanthoceras* from 'Ventnor' (BM(NH) 98206) may belong here, whilst some records of *Protacanthoceras compressum* from Wiltshire and Surrey (Wright & Wright 1951) may refer to this species. French records include the holotype from Provence and a specimen from the Rouen Fossil Bed figured by Kennedy & Hancock (1970 : pl. 97, figs 4a–b; BM(NH) C74796).

Protacanthoceras tuberculatum Thomel *mite* subsp. nov.

(Figs 3, 18–19)

1971 *Protacanthoceras* spp. nov. Kennedy : 103 (*pars*).

TYPES. The holotype, BM(NH) C81925, is a macroconch from the remanié phosphatic fauna of the Chalk Basement Bed at Ringstead (*Acanthoceras jukesbrownei* Zone). Paratypes BM(NH) C81926–8 are from the same horizon and locality and C81929–30 from the slightly older *Turrilites acutus* Zone Chalk Basement Bed at Lulworth Cove, Dorset; C81931–2 are from the *Acanthoceras jukesbrownei* Zone, Osmington landslips; C81933 (*ex* Mottram collection) is of the same age and from the same horizon below White Nothe; OUM K4425 is from the basal *Calycoceras naviculare* Zone Chalk Basement Bed at Askerswell.

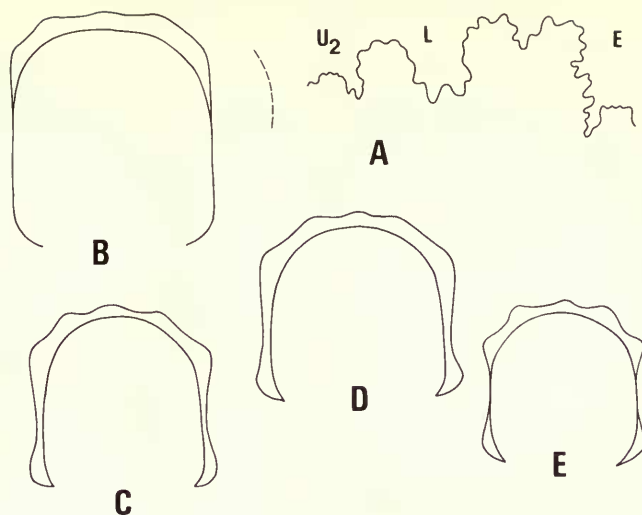


Fig. 3 *Protacanthoceras tuberculatum* Thomel mite subsp. nov. 3A, suture of BM(NH) C81926, $\times 4$. 3B, whorl section of BM(NH) C81925 at aperture of body chamber, $\times 2$. 3C, whorl section of BM(NH) C81929, $\times 2$. 3D, whorl section of OUM K4425, $\times 2$. 3E, whorl section of BM(NH) C81926, $\times 2$.

NAME. Latin *mitis*, mild, in reference to the difference in ornament between it and *P. t. tuberculatum*.

DIAGNOSIS. A subspecies of *Protacanthoceras tuberculatum* characterized by weak tuberculation, flank ribbing weak and slightly flexed or effaced and ventral tubercles only weakly clavate.

DESCRIPTION. This subspecies shows a similar size dimorphism to *P. t. tuberculatum*, with macroconchs adult at around 27–30 mm and microconchs generally at less than 25 mm. The umbilicus is generally smaller, 20% of diameter in juveniles, increasing to only 22% in mature individuals. The umbilical wall is vertical and rounded, with an abruptly rounded shoulder, the sides are flattened and subparallel in intercostal section, with the greatest breadth around mid-flank; the venter is broadly rounded. The costal section is more angular, with the greatest breadth at the umbilical bullae or inner ventrolateral tubercles. Relative proportions change throughout ontogeny, with the whorl breadth to height ratio ($Wb : Wh$) declining from 1.19 in specimens of 4–8 mm diameter to slightly less than unity in adults.

Juveniles have approximately 20 ribs per whorl, increasing to an estimated 22–24 at maturity. The arrangement of ribs and tubercles is as in *P. t. tuberculatum* but much feebler, the umbilical bullae consistently weaker, the ribs low, effaced at mid-flank and sometimes flexuous. The inner ventrolateral tubercles are generally weak, and always weaker than in the *P. t. tuberculatum*, as are the ventral ribs and tubercles. The latter are much less prominent, delicate and less elongated radially.

Modifications of the later parts of the mature body chamber are as in *P. t. tuberculatum* but with distinct flexure of ribbing in some individuals.

The suture is simpler than that of the nominate form, as shown in Fig. 3A.

DIMENSIONS. Percentage figures in brackets.

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb : Wh</i>	<i>U</i>
BM(NH) C81926	18.9 (100)	9.8 (52)	8.2 (43)	1.19	3.7 (20)
OUM K4425	22.4 (100)	10.5 (47)	10.3 (46)	1.02	4.4 (20)
BM(NH) C81929 {	—	11.5	12.1	0.95	—
—	—	10.5	10.3	1.02	—
BM(NH) C81927	26.5 (100)	11.9 (45)	11.8 (45)	1.0	5.3 (21)

DISCUSSION. Differences between *P. tuberculatum tuberculatum* and *P. t. mite* are brought out in the description. The subspecies is intermediate between *tuberculatum sensu stricto* and *P. arkelli* sp. nov. (p. 82), to which we believe it led by way of *arkelli verrucosum* subsp. nov. (p. 86); *mite* and *verrucosum* can be distinguished by virtue of the delicate but well-defined flank ribs of the latter, combined with delicate, barely clavate outer ventrolateral and siphonal tubercles and a stronger projection of ribs on the ventrolateral shoulder.

OCCURRENCE. Scarce in the *acutus*, *jukesbrownei* and basal *naviculare* Zone faunas of the Chalk Basement Bed in Dorset.

Protacanthoceras tuberculatum devonense subsp. nov.

(Figs 13, 36–40, 52)

1896 *Ammonites hippocastanus* var. *compressus* Jukes-Browne, in Jukes-Browne & Hill : 157 (*pars*); pl. 5, figs 3, 3a.

1970 *Protacanthoceras* spp. Kennedy : 660, 664, 666 (*pars*).

1971 *Protacanthoceras* sp. nov. Kennedy : 99 (*pars*); pl. 32, figs 4a–c.

1971 *Protacanthoceras* spp. nov. Kennedy : 103 (*pars*).

TYPES. The **holotype**, BM(NH) C81934, is a microconch from the remanié phosphatic fauna at the base of Division C of the Cenomanian Limestone, Whitlands; high *Calycoceras naviculare* Zone. Paratypes, from the same horizon and locality: BM(NH) C81935–7 and OUM K4461–72; in the Pinhay Humble Point–Whitlands Bay area: BM(NH) C7282, C73051, C73060, C81938–52, C81896, C81898 (labelled 'Chardstock' but clearly from the coast); GSM 53483, one of the syntypes of Jukes-Browne's *Ammonites hippocastanus* var. *compressus*; BM(NH) C81853 from the same horizon at the White Hart Sandpit, Wilmington; GSM Zn 9089, BM(NH) C81954 from Hooken Beach, Devon; C81955–6 from Hooken Cliff, Devon; numerous specimens in the O. H. Bayliss collection, from Shapwick Grange, Devon.

NAME. From the county of Devon.

DIAGNOSIS. A rectangular-whorled, depressed, coarsely ribbed *Protacanthoceras* with 12–15 alternately long and short ribs per whorl. Long ribs with strong conical umbilical tubercles, all ribs with strong conical inner ventrolateral tubercles and strongly clavate, closely-spaced, equal outer ventrolateral and siphonal tubercles.

DESCRIPTION. The coiling is involute on the inner whorls, the umbilicus 16–20% of the diameter, with a marked uncoiling of the body chamber to give a more evolute appearance at maturity, the umbilicus widening to 25% of the diameter (Fig. 42).

Figs 4–5 *Ammonites tropicus* Stoliczka, $\times 1$. 4a–c, BM(NH) C12590, *ex F.* A. Bather collection, from the *Calycoceras naviculare* Zone fauna of Bed C of the Cenomanian Limestone, Beer Head, Devon. 5a–b, copies of the original figures (Stoliczka 1865 : pl. 34, figs 2, 2a) of the holotype, from the Utatur Group near Odium, southern India.

Fig. 6a–b *Thomelites* aff. *sornayi* (Thomel), OUM K4443, *Calycoceras naviculare* Zone fauna of Bed C of the Cenomanian Limestone, Humble Point, Devon. $\times 1$.

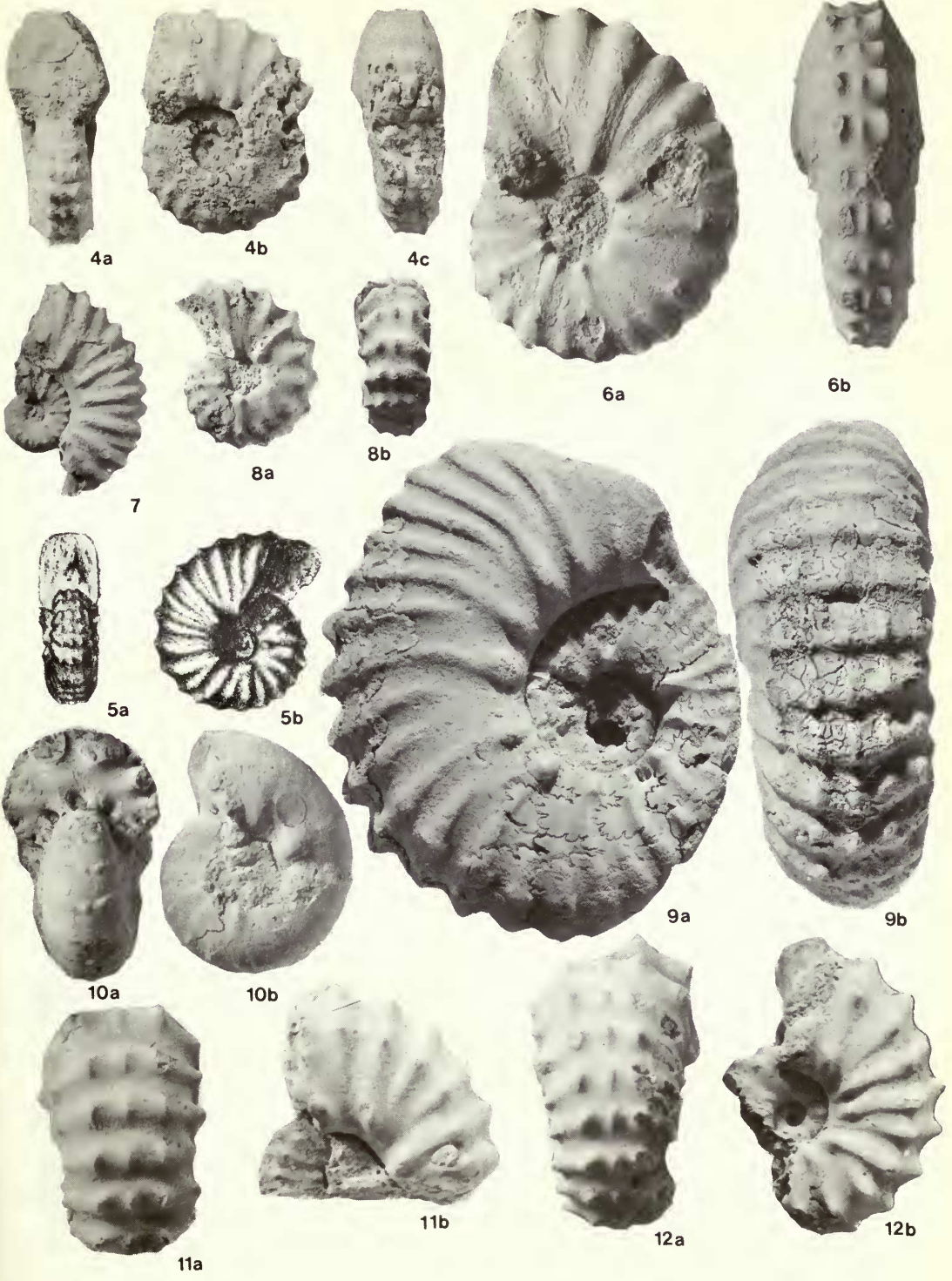
Fig. 7 *Calycoceras* (*Gentoniceras*) *gentoni* (Brongniart), OUM K4479, Chalk Basement Bed, *Turrilites acutus* Zone, Snowdon Hill, Chard, Somerset. $\times 1$.

Fig. 8a–b *Protacanthoceras tuberculatum tuberculatum* Thomel, OUM K4426, Chalk Basement Bed, *Calycoceras naviculare* Zone, Askerswell, Dorset. $\times 2$.

Fig. 9a–b *Pseudocalyoceras harpax* (Stoliczka) *ankomakaensis* Collignon, Ankomaka II (Manera), Madagascar. Original of Collignon 1964 : pl. 373, fig. 1621 (photographs supplied by W. A. Cobban). $\times 1$.

Fig. 10a–b *Nigericeras costatum* Barber, BM(NH) C47700, Lower Turonian, Pindiga, Nigeria. $\times 1$.

Figs 11–12 *Acanthoceras rhotomagense* (Brongniart), two juveniles from the *Turrilites costatus* Zone, base of Craie de Théligny, Sarthe, France (P. Juignet collection). $\times 2$.



Microconchs and macroconchs are essentially similar in ornament, with a size ratio of between 1 : 1.25 and 1 : 1.40. The umbilicus is of moderate depth, with a vertical, rounded wall and abruptly rounded shoulder. The whorls are depressed; the breadth to height ratio in intercostal section varies between 1.25 and 1.48, with the greatest breadth low on the flattened flanks and the venter flattened with broadly rounded shoulders. The breadth to height ratio ($Wb : Wh$) in the trapezoidal costal section varies from 1.19 to 1.48, with the greatest breadth at the umbilical tubercles. The ornament consists of 12–15 ribs per whorl, weaker on the phragmocone than on the body chamber and alternately long and short. Long ribs arise at the umbilical shoulder, originating in variable umbilical bullae, generally 7–8 per whorl, relatively weak on the phragmocone but stronger on the body chamber. They give rise to single, well-differentiated ribs, stronger on the body chamber, recti- or slightly prorsiradiate, straight, with strong conical inner ventrolateral tubercles. Thence, the ribs strengthen and project markedly across the shoulder to strong clavate outer ventrolateral tubercles, connected across the venter by a broad subdued rib bearing a clavate siphonal tubercle. The ventral tubercles are closely spaced and generally equal.

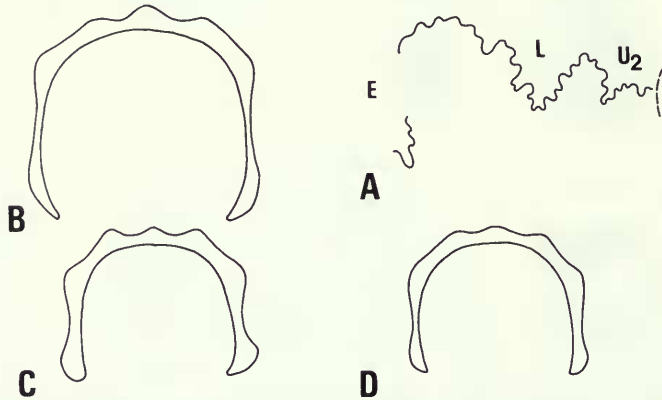


Fig. 13 *Protacanthoceras tuberculatum devonense* sp. nov. 13A, suture of BM(NH) C81935, $\times 4$. 13B, whorl section of body chamber of BM(NH) C81936, $\times 2$. 13C, whorl section of body chamber of BM(NH) C81935, $\times 2$. 13D, whorl section of body chamber of BM(NH) C81934, $\times 2$.

Most of the intercalated ribs arise low on the flank and may show a tenuous connection to an umbilical bulla. They are as strong as the major ribs and bear a similar complement of ventrolateral and siphonal tubercles. Some specimens also bear occasional intercalated ribs without inner ventrolateral tubercles.

Figs 14–17 *Protacanthoceras tuberculatum tuberculatum* Thomel. 14a–b, a juvenile, BM(NH) C81908 from the *Acanthoceras jukesbrownei* Zone fauna of the Chalk Basement Bed, Osmington, Dorset. 15a–d, BM(NH) C81904, and 17a–b, BM(NH) C81924, both macroconchs, from the same horizon and locality. 16a–b, BM(NH) C81922, from the Middle Cenomanian equivalent of Bed B of the Cenomanian Limestone at the White Hart Sandpit, Wilmington, Devon.

Figs 18–19 *Protacanthoceras tuberculatum mite* subsp. nov. 18a–c, BM(NH) C81929, a macroconch body chamber from the *Turrilites acutus* Zone fauna of the Chalk Basement Bed at Lulworth Cove, Dorset. 19a–c, **holotype** BM(NH) C81925, a macroconch from the *Acanthoceras jukesbrownei* Zone fauna of the Chalk Basement Bed, Ringstead Quarry, Dorset.

Figs 20–21 *Protacanthoceras asgeirri* sp. nov., both from the basal *Calycoceras naviculare* Zone fauna of the Chalk Basement Bed at Askerswell, Dorset. 20a–c, paratype, OUM K4434. 21a–d, **holotype**, OUM K4433.

Fig. 22a–b *Protacanthoceras tuberculatum* Thomel. OUM K4439, the subspecifically indeterminate nucleus of an individual from the *Turrilites acutus* Zone fauna of the Chalk Basement Bed at Snowdon Hill, Chard, Somerset.

All figures are $\times 1.125$.



14a

14b

15a

15b

15c



16a

16b

15d

17a

17b



18a

18b

18c

19a

19b

19c



20a

20b

20c

21a

21b

21c

21d

22a

22b

The subspecies shows typical adult features, consisting of a decline in the umbilical bullae and a strengthening of the ventrolateral and ventral ribbing at the expense of the tubercles.

The suture is of basic rather simple *Protacanthoceras* type, with little-divided bifid elements (Fig. 13A).

DIMENSIONS. Typical specimens are as follows; percentage figures in brackets.

	D	Wb	Wh	Wb : Wh	U	Ribs per whorl
BM(NH) C81934 at c	20.8 (100)	11.5 (55)	8.0 (38)	1.43	5.3 (25)	12
Ic	20.8 (100)	9.9 (48)	6.7 (32)	1.48	5.3 (25)	14
BM(NH) C81935 at c	17.9 (100)	10.5 (59)	7.1 (40)	1.48	4.2 (23)	14
Ic	17.9 (100)	8.9 (50)	6.6 (37)	1.35	4.2 (23)	—
BM(NH) C81936 at c	25.0 (100)	12.8 (51)	10.8 (43)	1.19	5.0 (20)	7 ($\frac{1}{2}$ whorl)
Ic	25.0 (100)	11.5 (46)	9.2 (37)	1.25	5.0 (20)	—

DISCUSSION. Typical *P. tuberculatum devonense* are readily separable from other forms such as *P. bunburianum* and *P. tuberculatum tuberculatum* by their coarse, sparse ribs and strong tuberculation. Some variants (e.g. Figs 36, 52) show rather subdued ornament and a rounding of the venter which recall *Protacanthoceras proteus proteus* and *P. p. baylissi*, but all possess distinctive ventrolateral and ventral tuberculation throughout ontogeny and are easily recognizable.

P. t. devonense originated in *P. t. tuberculatum* by decrease in size, coarsening of ribbing and tuberculation and a great reduction in rib density.

OCCURRENCE. This subspecies is widespread in the *Calycoceras naviculare* Zone faunas of Division C of the Cenomanian Limestone and its equivalents in Devon.

Protacanthoceras tuberculatum cyclopeum subsp. nov.

(Figs 34, 45)

TYPES. The holotype is BM(NH) C81299, formerly Col. O. H. Bayliss' coll. no. 193; a paratype remains in the same collection. Both are from the remanié phosphatic fauna at the base of Division C of the Cenomanian Limestone, high *Calycoceras naviculare* Zone, Shapwick Grange, Devon.

NAME. Latin *cyclopeus*, in allusion to the size and locality (Shapwick = sheep farm) of the holotype; cyclopes were giants and the best known, Polyphemus, kept sheep.

DIAGNOSIS. A large (52 mm diameter) subspecies of *P. tuberculatum* with 16 broad, blunt, alternately long and short ribs per whorl. Long ribs bear strong conical umbilical bullae; all ribs bear prominent inner ventrolateral tubercles which are stronger on long ribs than intercalated ribs, whilst ventral tuberculation declines and strong ventral chevron-ribbing develops on the apertural parts of the mature body chamber.

DESCRIPTION. The holotype is a well-preserved, phosphatic internal mould, with just under two-thirds of a whorl of body chamber. The last few septa are crowded and overlap, suggesting the specimen to be a mature adult.

The coiling is evolute, becoming increasingly so on the outer whorl, where the umbilical seam of the body chamber egresses somewhat so that, at the aperture, c. 40% of the previous whorl is covered. The umbilicus is of moderate size (c. 30% of diameter) with a rounded wall of moderate elevation and an abruptly rounded shoulder. The whorl section is depressed. The flanks are flat intercostally, with the maximum breadth on the inner third of the whorl side. The outer third of the flanks converge somewhat; the ventrolateral shoulder is rounded and the venter somewhat flattened. The costal section is more angular, with the greatest breadth on the phragmocone at the spinose lower ventrolateral tubercle and on the body chamber at the umbilical bulla.

There are eight strong, conical to bullate umbilical tubercles per whorl, positioned on the umbilical shoulder and extending to the umbilical seam as broad, rounded, subdued swellings. From the bullae arise single, broad, relatively low, rounded and more or less radial ribs which pass straight across the flanks to connect to prominent subspinose inner ventrolateral tubercles. These are very prominent on the earlier portions of the outer whorl, become less prominent and

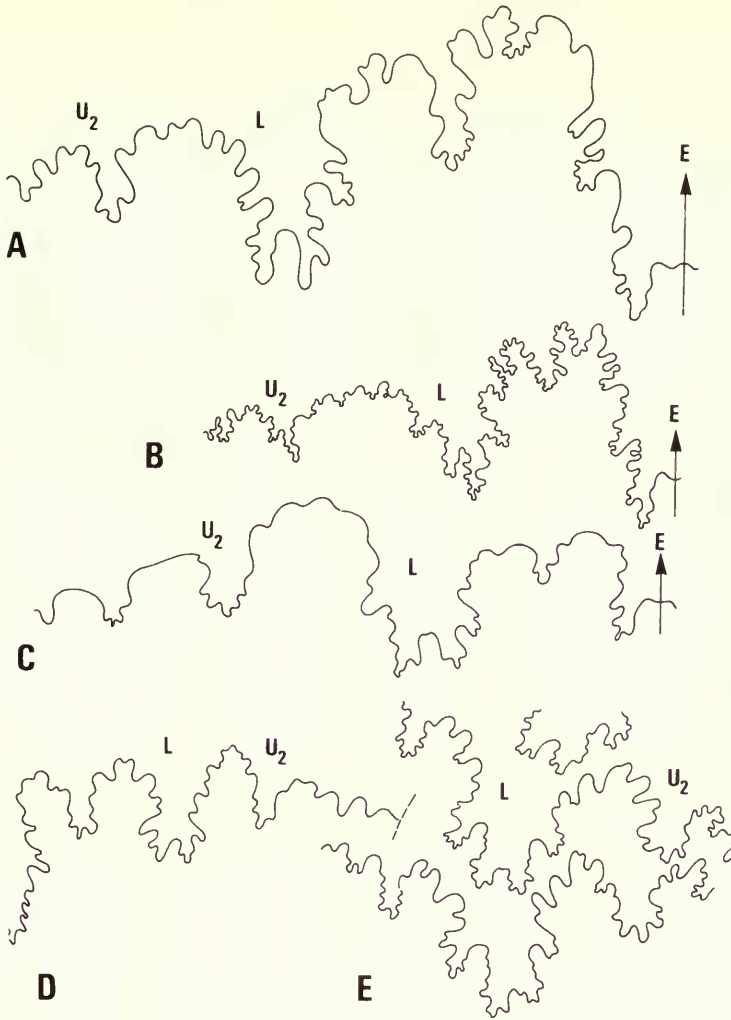


Fig. 23 Suture lines of selected mature acanthocerataceans compared. 23A, *Acanthoceras rhotomagense* (Brongniart). P. Juignet coll. no. 1-161, from the phosphatic *Turrilites costatus* Zone fauna at the base of the Craie de Théligny, Sarthe, France, $\times 4$. 23B, *Calycoceras naviculare* (Mantell). OUM K4442, *Calycoceras naviculare* Zone fauna of Division C of the Cenomanian Limestone, Humble Point, Devon, $\times 2$. 23C, *Metoicoceras geslinianum* (d'Orbigny). OUM KT22, *Sciponoceras gracile* Zone, Eagle Ford Shale, Dallas/Fort Worth, Texas, $\times 2$. 23D, *Pseudocalycoceras* aff. *dentonense* (Moreman). *Sciponoceras gracile* Zone, Ikushumbets, Hokkaido (modified after Matsumoto & Kawano 1975: text-fig. 3), $\times 2$. 23E, *Thomelites* aff. *sornayi* (Thomel). OUM K4443, *Calycoceras naviculare* Zone, Division C of the Cenomanian Limestone, Humble Point, Devon, $\times 2$.

subdued, with a tendency towards clavation on the early parts of the body chamber, declining towards the aperture. From them a broad rounded, straight rib passes forwards across the ventrolateral shoulder to strong clavate siphonal tubercles, sharp at the smallest diameters visible but declining on the body chamber and merging with the inner ventrolateral tubercles into strong transverse and elevated ribs. Low broad ribs extend across the venter and bear a strong clavate siphonal tubercle, somewhat more elongate than the outer ventrolateral. This tubercle declines towards the body chamber but retains its identity to the aperture. Shorter ribs, arising low on the flank and lacking umbilical bullae (although some connect tenuously to the bulla of

the long ribs next to them), alternate regularly with the longer ribs. These intercalated ribs bear the same complement of ventrolateral and ventral tubercles as the long ribs, but the inner ventrolateral tubercles are always weaker than the corresponding ones on the long ribs.

Modifications of the adult body chamber include a sudden decline of umbilical bullae, weakening and crowding of ribs, development of striae and a fusion of inner and outer ventrolateral tubercles into obliquely placed bar-like ribs, which, with broadening and accentuation of the ventral ribbing, give the venter a scale-like appearance.

The suture line is quite deeply subdivided for the genus, with a deep and relatively narrow E, a deep, narrow, asymmetrically bifid L and a much smaller U₂. E/L is broad and asymmetrically bifid; L/U₂ is symmetrically bifid.

DIMENSIONS. Percentage figures in brackets.

	D	Wb	Wh	Wb : Wh	U
BM(NH) C81299	51.9 (100)	23.2 (45)	20.9 (40)	1.11	15.3 (29)
at c	42.5 (100)	22.8 (54)	17.8 (42)	1.28	12.1 (28)
Ic	42 (100)	20.7 (49)	15.8 (37)	1.31	12.1 (28)
at c	38.0 (100)	15.6 (41)	11.0 (29)	1.42	11.5 (30)
Ic	38.0 (100)	11.9 (31)	9.4 (25)	1.27	11.5 (30)

DISCUSSION. *P. tuberculatum cyclopeum* is the largest form of *Protacanthoceras* we have seen. It is readily differentiated from its contemporaries, in that *P. proteus proteus* and *P. p. baylissi* are round-whorled, with quite distinctive changes in ornament, whilst *P. bunburianum* and its variants have a compressed whorl section and finer ornament, and are much smaller.

P. t. cyclopeum is like an extremely large *P. t. tuberculatum* Thomel (Figs 14–17), but is separable not only because of its size, well outside that of populations of the latter before us, but also by having fewer ribs and coarser ornament; furthermore in *P. t. tuberculatum* tubercles are similar on all ribs, whilst in *P. t. cyclopeum* ribs are generally sharply differentiated from much flatter flanks.

OCCURRENCE. As for types.

Protacanthoceras arkelli sp. nov.

TYPES. The **holotype**, BM(NH) C81957, is a macroconch from the remanié phosphatic fauna of the Chalk Basement Bed, Ringstead Quarry, *Acanthoceras jukesbrownei* Zone. Paratypes, all microconchs, are BM(NH) C81958–9 from the same horizon and locality, and C81960–1, from the same horizon in the Osmington landslips.

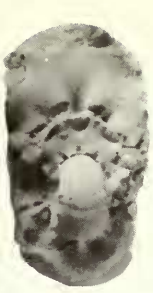
NAME. After the late W. J. Arkell, at whose Ringstead house the collector of the holotype (C.W.W.) was staying at the time.

Figs 24–26 *Protacanthoceras arkelli arkelli* subsp. nov., all from the *Acanthoceras jukesbrownei* Zone fauna of the Chalk Basement Bed at Ringstead, Dorset. 24, BM(NH) C81961, showing details of the inner whorls, $\times 1.5$. 25a–d, **holotype**, BM(NH) C81957, a macroconch, $\times 1.125$. 26a–b, BM(NH) C81958, microconch paratype, $\times 1.125$.

Fig. 27a–c *Protacanthoceras arkelli verrucosum* subsp. nov. **Holotype**, BM(NH) C81962, from the *Acanthoceras jukesbrownei* Zone fauna of the Chalk Basement Bed at Ringstead Quarry, Dorset. $\times 1.125$.

Fig. 28 *Protacanthoceras tuberculatum* Thomel, subspecies undetermined. Inner whorls of OUM K4429, from the basal *Calycoceras naviculare* Zone of Askerswell, Dorset. $\times 1.5$.

Figs 29–33 *Protacanthoceras bunburianum* (Sharpe). Figs 29–30, 32–33 from the *Calycoceras naviculare* Zone fauna of Bed C of the Cenomanian Limestone, Humble Point, Devon. Juvenile microconchs: 29a–b, OUM K4445, and 30a–b, BM(NH) C81968. Macroconchs: 32a–d, BM(NH) C81969, and 33a–b, BM(NH) C81965. Fig. 31a–d, holotype, BM(NH) 50155, figd Sharpe 1853 : pl. 9, figs 3a–c. An adult macroconch, said to be from Chardstock, Devon, but more likely to be from the *Calycoceras naviculare* Zone fauna of Bed C of the Cenomanian Limestone of the Devon Coast (see Kennedy 1971 : 98 for discussion). All $\times 1.125$.



24



25a



25b



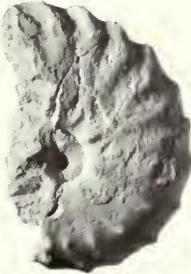
25c



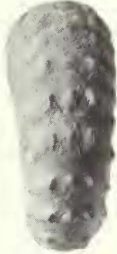
25d



27a



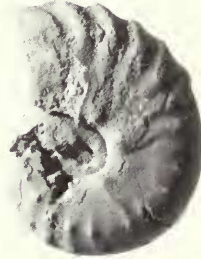
27b



27c



26a



26b



29a



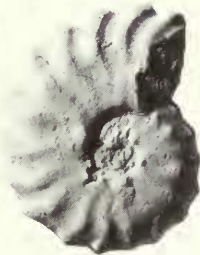
29b



28



30a



30b



31a



31b



31c



31d



32a



32b



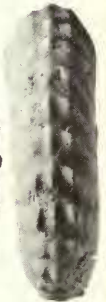
32c



32d



33a



33b

DIAGNOSIS. An involute, compressed *Protacanthoceras* characterized by very weak to obsolete flank ribs and delicate lateral and ventral tuberculation, which latter may disappear during middle growth. The body chamber develops well-defined lateral and ventral ribbing only towards the adult apertural margin.

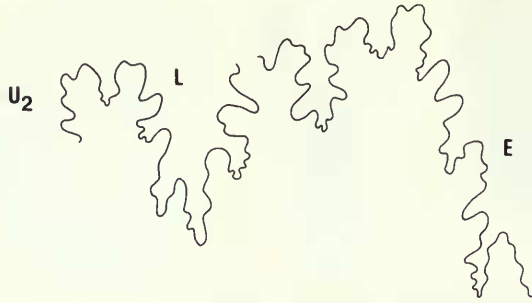


Fig. 34 *Protacanthoceras tuberculatum cyclopeum* subsp. nov. Suture of holotype, BM(NH) C81299 (OB 193), $\times 4$.

Protacanthoceras arkelli arkelli subsp. nov.
(Figs 24–26, 35A–H)

? 1970 *Protacanthoceras* sp. Kennedy & Hancock: pl. 97, figs 7a–b.

TYPES. As above.

DIAGNOSIS. An involute, compressed subspecies of *P. arkelli* with an initial stage characterized by delicate umbilical bullae which give rise to groups of delicate falcon ribs bearing tiny inner and outer ventrolateral and siphonal tubercles, a second growth stage in which outer ventrolateral and siphonal tubercles disappear, their place being taken by spiral striae, and a third stage in which distinct crowded ribs, stronger than those of the earlier stage, reappear bearing weak umbilical bullae and well-developed ventrolateral and siphonal tubercles. On the latter part of the body chamber the ventral ribs are strong and the outer ventrolateral and siphonal clavi virtually disappear. Microconch and macroconch are essentially similar, with a size ratio of 1 : 1.3.

DESCRIPTION. The holotype is a well-preserved phosphatic internal mould of a macroconch, retaining traces of iridescent phosphatized shell. The last few sutures are crowded, suggesting the specimen is adult, whilst the last two-thirds of the outer whorl are body chamber, showing modifications indicating the specimen to be a mature adult.

Two specimens, C81959 and C81961, show nuclei at diameters of 4–6 mm (Figs 24, 34G, H). At this stage, the coiling is moderately involute, with a small, relatively deep umbilicus and a depressed reniform whorl section.

The flanks bear low, broad, sparse ribs, *c.* 10 per whorl, strengthened into bullate tubercles at the umbilical shoulder and terminating in relatively strong conical ventrolateral tubercles. The venter of C81959 is smooth and completely lacks ribs; on the inner whorls of C81961 there are periodic broad chevron-like constrictions at intervals of two per half-whorl (Fig. 24); behind one of these constrictions there is a low rib. *P. arkelli arkelli* undergoes distinctive morphological changes during middle and late growth. Up to 15–20 mm, the coiling is involute, with over half the previous whorl being covered. The umbilicus is small, < 20% of diameter, of moderate depth with a flattened vertical wall and an abruptly rounded shoulder. The whorls are compressed and flat-sided (breadth to height ratio *Wb* : *Wh* *c.* 0.9) with the greatest breadth at the umbilical bulla. The sides are more or less parallel and the venter broad and strongly convex. Ornament consists of 7–8 weak, comma-shaped umbilical bullae, from which arise low, weak, gently flexed ribs or striae in groups of two or three; occasional shorter intercalated ribs are also present low on the flanks as mere striae. All ribs bear small, delicate, sharp, conical inner ventrolateral tubercles at the junction of the flattened sides and the arched venter. These give rise to a much

broader, flat-topped rib which passes forwards across the ventrolateral tubercles. These in turn are connected by a very subdued transverse rib, which bears a small but clearly differentiated and somewhat clavate siphonal tubercle.

From 15–20 mm to the early parts of the body chamber the proportions, coiling and whorl sections remain unchanged. However, the flank ribs become subdued, the inner ventrolateral tubercles are slightly weakened and virtually all of the remaining ventral ornament becomes suddenly weaker, leaving a smooth rounded venter (Figs 25b, 26a) ornamented by delicate transverse and low spiral ridges and striae, the former corresponding in position to outer ventrolateral and siphonal tubercles. Where transverse striae and spiral ridges intersect, there is the merest suggestion of an incipient tubercle.

On the later portions of body chamber there is a revival of ornament that is as abrupt as the previous decline. Umbilical bullae give rise to two or three faint, low, broad ribs, with occasional additional ribs intercalated. Inner ventrolateral tubercles become stronger and are joined by a strong, forward-directed rib across the ventrolateral shoulder to markedly clavate outer ventrolateral tubercles. A low, broad rib extends across the venter (Figs 25d, 26a) and bears a distinct to subdued siphonal tubercle. Towards the aperture, ventral and ventrolateral ribbing becomes stronger and all tuberculation declines, to give the distinct *Protacanthoceras* ventral ribbing (Fig. 25a).

The sutures (Fig. 35A, B) are of the basic, rather simple *Protacanthoceras* type, with a deep and rather narrow E, bifid and relatively broader L and a very small U_2 . E/L is asymmetrically bifid,

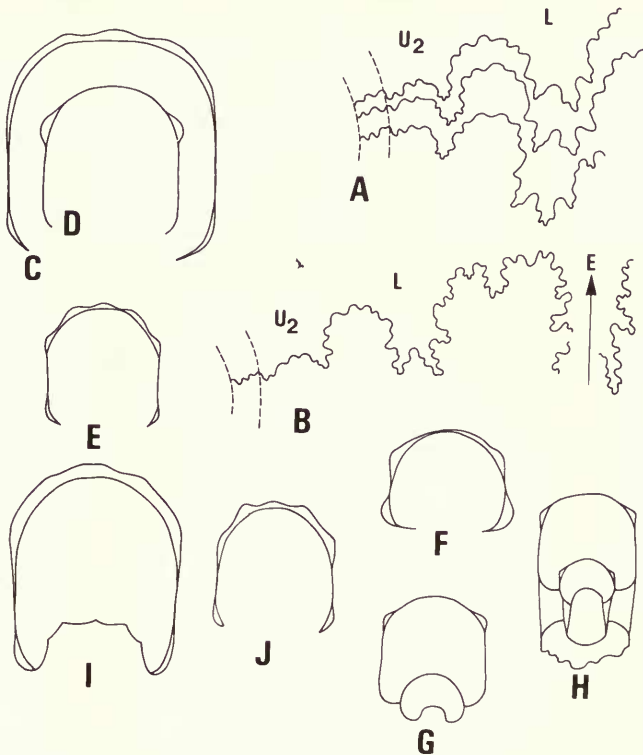


Fig. 35 *Protacanthoceras arkelli* sp. nov. 35A–H, *Protacanthoceras arkelli arkelli*. 35A, adult sutures of BM(NH) C81957, $\times 4$. 35B, suture of BM(NH) C81958, $\times 4$. 35C, D, whorl sections of BM(NH) C81957 at aperture and at tuberculate stage, $\times 2$. 35E, whorl section of BM(NH) C81958 at tuberculate stage, $\times 2$. 35F, whorl section during early development shown by BM(NH) C81959, $\times 2$. 35G, H, whorl sections during early development as shown by BM(NH) C81961, $\times 2$. 35I–J, *Protacanthoceras arkelli verrucosum* subsp. nov. Whorl sections of BM(NH) C81962, $\times 2$.

L/U₂ is very little divided, whilst there is a series of small, smoothly rounded frills on the suspensive lobe.

DIMENSIONS. Percentage figures in brackets.

	D	Wb	Wh	Wb : Wh	U
BM(NH) C81957	28.2 (100)	11.8 (42)	12.5 (44)	0.94	5.5 (19.5)
at	21.2 (100)	9.1 (43)	10.6 (50)	0.89	4.1 (19.3)
BM(NH) C81958	22.8 (100)	9.9 (43)	10.5 (46)	0.94	4.3 (19.0)

DISCUSSION. The very distinctive ontogenetic changes shown by *P. arkelli arkelli*, and its weak flank ornament, compressed whorl section and rounded venter serve to distinguish it from all other described *Protacanthoceras* species. It differs from *P. arkelli verrucosum* subsp. nov. (below) in the presence of an intermediate growth stage during which ventral ornament declines; *verrucosum* retains a full complement of tubercles throughout ontogeny.

There is very striking resemblance between the very earliest stages of *Protacanthoceras tegulicium* (p. 88) and the second growth stage of *P. arkelli arkelli*, both showing a smooth arched venter, distinct tubercles at the juncture of venter and flank and distinctive flank ribs (compare Fig. 44 with 24). As discussed below, this may be the key to the origin of the otherwise very distinctive *P. tegulicium*.

OCCURRENCE. As for type material. The specimen of *Protacanthoceras* from the Rouen Fossil Bed figured by Kennedy & Hancock (1970 : pl. 97, figs 7a–b) may be a poorly preserved *P. arkelli arkelli*.

Protacanthoceras arkelli verrucosum subsp. nov.

(Figs 27, 35I, J)

TYPES. The **holotype**, BM(NH) C81962, is a microconch (?), from the remanié phosphatic fauna of the Chalk Basement, *Acanthoceras jukesbrownei* Zone, Ringstead Quarry. Paratype OUM K4440 is from the *Turrilites acutus* Zone fauna of the Chalk Basement Bed at Snowdon Hill, Chard.

NAME. In reference to the subspecies' distinctive delicate tubercles. One meaning of *verruca* is an excrescence on a precious stone (Pliny).

DIAGNOSIS. A subspecies of *Protacanthoceras arkelli* in which inner and outer ventrolateral and siphonal tubercles with associated ribs are retained throughout development, declining only at the mature aperture.

DESCRIPTION. The holotype is a phosphatic internal mould, retaining traces of iridescent phosphatized shell. It consists of all the body chamber and a nucleus (which is poorly visible). Changes in ornament on the body chamber suggest that the specimen is adult.

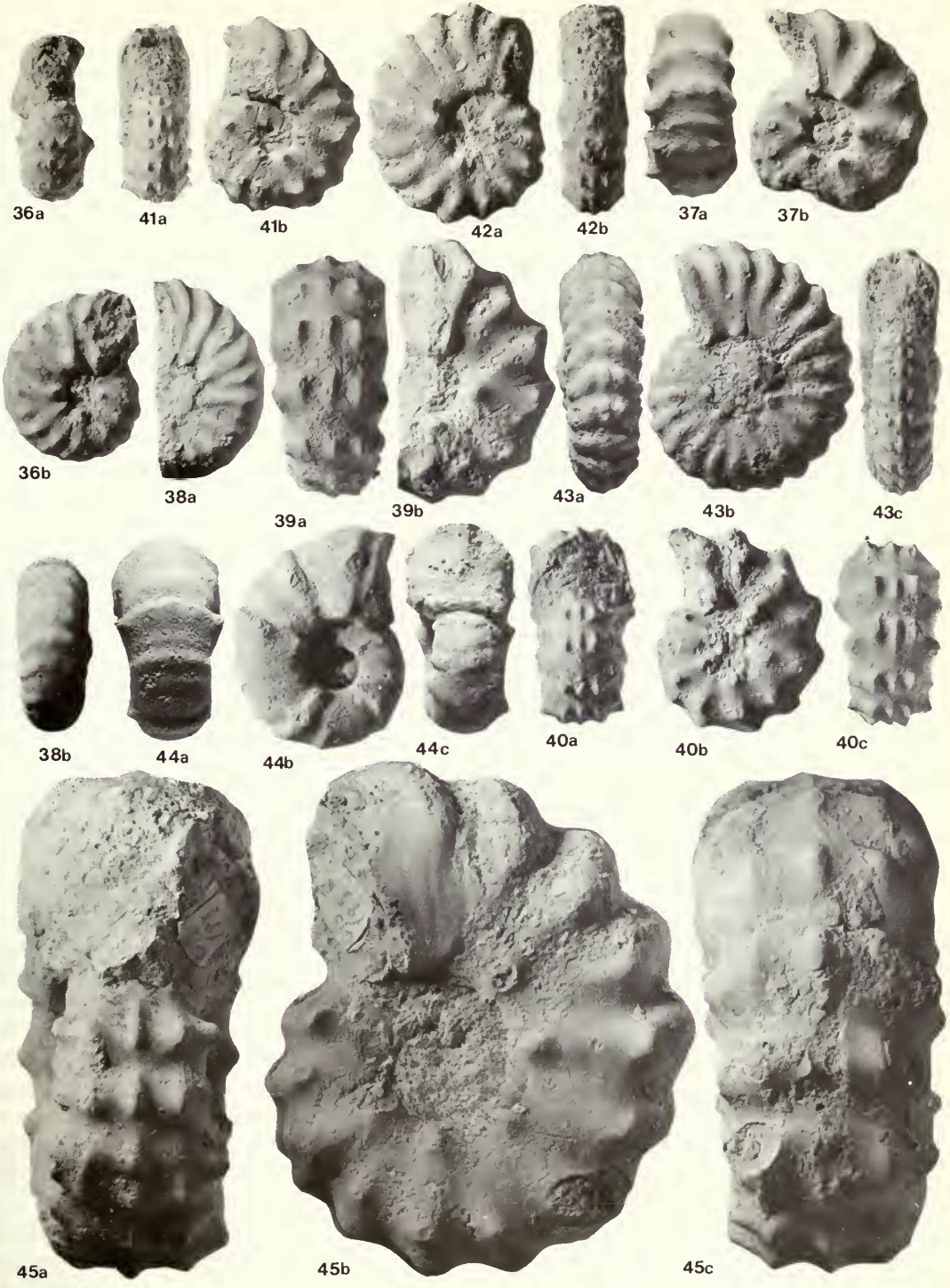
Figs 36–40 *Protacanthoceras tuberculatum devonense* subsp. nov., all from the *Calycoceras naviculare* Zone fauna of Bed C of the Cenomanian Limestone. Figs 36, 37 and 39 are from Humble Point, Fig. 38 from Shapwick Grange and Fig. 40 from Pinhay Bay, all in Devon. 36a–b, BM(NH) C81937, and 37a–b, BM(NH) C81935, microconchs. 38a–b, BM(NH) C81302 (ex O. H. Bayliss coll. no. OB 271), a microconch transitional to *P. proteus baylissi* subsp. nov. 39a–b, BM(NH) C81936, a macroconch paratype. 40a–c, **holotype**. BM(NH) C81934, a microconch.

Figs 41–43 *Protacanthoceras bunburianum* (Sharpe), all from the *Calycoceras naviculare* Zone fauna of Division C of the Cenomanian Limestone. Fig. 41 from near Whitlands, Fig. 42 from Hooken Beach, and Fig. 43 from Humble Point, all in Devon. 41a–b, BM(NH) C81992, and 42a–b, BM(NH) C81999, both microconchs. 43a–c, BM(NH) C81967, a macroconch.

Fig. 44a–c *Protacanthoceras tegulicium* sp. nov. **Holotype**, OUM K4435, from the basal *Calycoceras naviculare* Zone fauna of the Chalk Basement Bed at Askerswell, Dorset.

Fig. 45a–c *Protacanthoceras tuberculatum cyclopeum* subsp. nov. **Holotype**, BM(NH) C81299 (ex O. H. Bayliss coll. no. OB 193), from the *Calycoceras naviculare* Zone fauna of Bed C of the Cenomanian Limestone at Shapwick Grange, Devon.

All figures are $\times 1.125$.



The coiling is involute, over half the previous whorl being covered. The umbilicus is small (19% of diameter) and of moderate depth. The umbilical wall is vertical, rounded, with an abruptly rounded shoulder. The whorl sides are flattened; the greatest breadth is at the umbilical bulla at the beginning of the body chamber but towards the ventrolateral shoulder at the aperture. The venter is broadly rounded in intercostal but more flattened in costal section (Fig. 35J). There are five small umbilical bullae on the half whorl of body chamber. From these arise pairs of gently flexed, radial ribs, very subdued at the middle of the flank, being sometimes reduced to mere striae, but stronger and broader across the outer flank. There are occasional intercalated ribs which arise low on the flank and may extend to the umbilicus as mere striae. In all there are 13 ribs on the last half whorl.

All but the last few ribs bear distinct, sharp, conical inner ventrolateral tubercles, whence arise broader, stronger ribs, which project forwards across the ventrolateral shoulder to sharp, distinctly clavate outer ventrolateral tubercles. A low subdued rib extends across the venter, bearing a clavate siphonal tubercle. Modifications of the last few ribs towards the mature aperture include a strengthening of the ventral and ventrolateral portion into a strong rounded rib and a decline of the inner ventrolateral tubercles to virtual obsolescence, and a loss in identity and definition by the outer ventrolateral and siphonal tubercles.

The holotype is broken across the last septum and the suture is damaged; it appears to have been simple and of basic *Protacanthoceras* design.

DIMENSIONS. Percentage figures in brackets.

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb : Wh</i>	<i>U</i>
BM(NH) C81962	24.5 (100)	10.4 (42)	11.2 (46)	93	47 (19)

DISCUSSION. *P. arkelli verrucosum* differs from the nominate form in retaining distinctive inner and outer ventrolateral and siphonal tubercles with associated ventral and ventrolateral ribbing, as compared to the smooth-ventered second growth stage of *arkelli arkelli*, which generally extends to at least the early parts of the body chamber. *P. tuberculatum tuberculatum* and *P. t. mite* are robust, coarsely-ribbed forms by comparison, in which the ventral tubercles are markedly pinched and clavate. *P. arkelli verrucosum* is morphologically transitional in many respects between *P. tuberculatum mite* and *P. arkelli arkelli*, but the specimens come from a condensed Basement Bed facies and there is no stratigraphic evidence for or against this inferred relationship.

OCCURRENCE. As for types.

Protacanthoceras tegulicium sp. nov.

(Figs 44, 46)

1970 *Protacanthoceras* sp. Kennedy : 644.

1971 *Protacanthoceras* spp. nov. Kennedy : 103 (*pars*).

HOLOTYPE. OUM K4435 from the Chalk Basement Bed, low *Calycoceras naviculare* Zone, at Askerswell, Dorset.

NAME. Late Latin *tegulicium*, tiled, a reference to the imbricate appearance of the venter, the ribs upon which resemble overlapping roof tiles.

DIAGNOSIS. Whorl section reniform. No siphonal or outer ventrolateral tubercles, but with periodic strengthened primary ribs bearing subspinose umbilical bullae and inner ventrolateral tubercles at maturity. The strengthened primaries have a shallow rear and steep front slope giving the appearance of constrictions. These ribs are separated by two or three weaker, untuberculated ribs.

DESCRIPTION. The holotype is a phosphatic internal mould retaining traces of iridescent phosphatized shell. The specimen is adult, and two-thirds of the outer whorl is body chamber.

The coiling is moderately evolute, with almost half of the previous whorl covered. The umbilicus is moderately broad (31% of diameter) and of moderate depth. The whorl section is slightly depressed (*Wb : Wh* is 1.28 at a diameter of 22.2 mm), reniform in intercostal section (Fig. 46B)

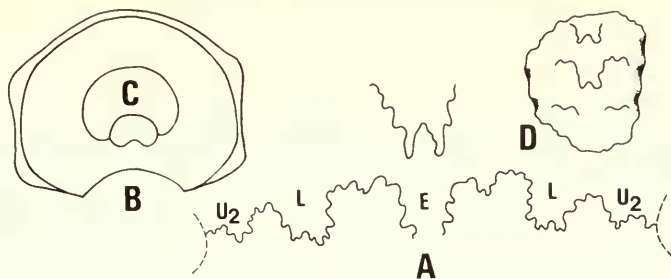


Fig. 46 *Protacanthoceras tegulicium* sp. nov., based on the holotype, OUM K4435. 46A, suture, $\times 4$. 46B, whorl section of body chamber, $\times 4$. 46C, whorl section of nucleus, $\times 8.3$. 46D, early sutures on nucleus, $\times 8.3$.

with the flanks strongly rounded and the venter flattened and broadly rounded, the greatest breadth quite low on the flank. The costal section is more angular, flat or even concave on the flanks, with sharp subspinose umbilical and ventral corners and a slight concavity on either side of a broadly rounded venter. The greatest breadth is at the ventrolateral angle.

There are ten irregularly-spaced primary ribs on the outer whorl. These arise as the faintest swellings at the umbilical seam. They develop into sharp, pointed bullae at the umbilical shoulder, which become stronger progressively towards the aperture. The ribs are strong, rounded, recti- to slightly prorsiradiate, low at mid-flank and produced into sharp inner ventrolateral tubercles, which become very strongly developed towards the aperture. At the smallest diameters visible, there are no obvious outer ventrolateral tubercles, although an almost imperceptible deflection of rib direction occurs on some ribs at the outer ventrolateral position. The ribs are strong and rounded, with very shallow rear and steep front slopes, and pass across the venter with a slight forward sweep, in some cases forming a distinct obtuse angle at mid-venter (Fig. 44a).

Between the main ribs are two or three low, relatively broad ribs best developed across the venter, lacking all trace of tubercles. These ribs pass straight across the venter.

The mature adult aperture shows typical *Protacanthoceras* modifications: there is a strong, tuberculate rib followed by a deep intercostal depression; the aperture itself is simple, slightly flared and projected into a short but distinct angular rostrum.

The nucleus was removed during preparation and shows inner whorls (Fig. 46C–D) which are depressed and reniform at a whorl breadth of 1.5 mm., with low, broad ribs on the flank, and a broadly rounded flattened venter quite without tubercles, although crossed by faint striations. At a whorl breadth of 0.8 mm the whorl is depressed and quite without ornament.

The mature suture consists of a deep and relatively narrow E, with a linguiform, little-divided median saddle, less than half as long as high. E/L is broad, asymmetrically bifid, with very minor incisions. L is broad and asymmetrically bifid; L/U₂ is small and little divided, whilst U₂ is very small. There are two very simple auxiliaries on the suspensive lobe external to the umbilical seam.

DIMENSIONS. Percentage figures in brackets.

	D	Wb	Wh	Wb : Wh	U
OUM K4435	22.2 (100)	11.8 (53)	9.2 (41)	1.28	6.9 (31)

DISCUSSION. Although represented only by the holotype, this extraordinary species is highly distinctive, with its lack of siphonal and outer ventrolateral tubercles and its *Peltoceras*-like ribs and tubercles. It most closely resembles the later *P. proteus* sp. nov. (Fig. 50), but *proteus* has a more rounded whorl section, has much more subdued inner ventrolateral tubercles and bears small but distinct clavate siphonal and outer ventrolateral tubercles during early growth. *P. proteus baylissi* (Fig. 51), although equally lacking siphonal tubercles, also lacks ventrolateral tuberculation and has a much more rounded whorl section.

The origin of *Protacanthoceras tegulicium* is fairly clearly established in *Protacanthoceras arkelli*,

whose nucleus, with broad rounded venter, chevron-like constrictions and flank ribs with strong ventral tubercles is in many respects a miniature *tegulicium*.

OCCURRENCE. As for holotype.

Protacanthoceras asgeirri sp. nov.
(Figs 20–21, 47)

1970 *Protacanthoceras* sp. b Kennedy : 644.

1971 *Protacanthoceras* spp. nov. Kennedy : 103 (*pars*)

TYPES. The **holotype**, OUM K4433, is from the Chalk Basement Bed, low *Calyoceras naviculare* Zone, at Askerswell, Dorset. A paratype, OUM K4434, is from the same horizon and locality.

NAME. From the type locality, Askerswell, deriving from the Old Norse name Asgeirr.

DIAGNOSIS. A small round-whorled *Protacanthoceras*, the middle growth stages characterized by low distant primary ribs with umbilical bullae and subdued, rounded inner and outer ventrolateral and siphonal tubercles and shorter intercalated non-tuberculate ribs. Later growth stages characterized by loss of all ventrolateral and ventral tuberculation, leaving relatively strong umbilical bullae and primary ribs separated by two or three intercalated short ribs.

DESCRIPTION. The holotype is a slightly corroded phosphatic internal mould retaining traces of phosphatized shell. The specimen is adult and two-thirds of the outer whorl is body chamber.

The coiling is moderately involute on the phragmocone, becoming rather more evolute on the outer whorl, the body chamber uncoiling somewhat so that the width of the umbilicus is 26% of the total diameter. The umbilicus is of moderate depth with a vertical wall and abruptly rounded shoulder. The breadth and height are more or less the same, the flanks subparallel, with an evenly rounded arched venter (Fig. 47B). There are seven umbilical bullae on the last half whorl (all of which is body chamber) and an estimated twelve per whorl. On the phragmocone and early parts of the body chamber these bullae give rise to low, broad, gently flexed prorsiradiate ribs, which are strengthened on the shoulder into subdued bullae. From these the ribs become broader and stronger and sweep forwards across the ventrolateral shoulder to faint, low, rounded to transversely elongate outer ventrolateral tubercles. These are linked by a low broad rib, projected across the venter in a marked sinus, and bearing a faintly discernible, rounded siphonal tubercle. Between these strong primary ribs are faint, non-tuberculate ribs and striae, two or three between each tuberculate pair. This type of ornament extends onto the earlier parts of the body chamber. On later parts, ventral and ventrolateral tuberculation declines, but the umbilical bullae become stronger, as do the ribs. The flanks are thus ornamented by long, clearly differentiated broad ribs and one or two intercalated shorter ribs between each pair of long ribs. All ribs sweep forwards across the ventrolateral shoulder but cross the centre of the venter in a shallow curve.

The last few sutures are approximated, indicating the specimen to be mature. No details can be deciphered other than very simple lobes and saddles in a suture of basic *Protacanthoceras* pattern.

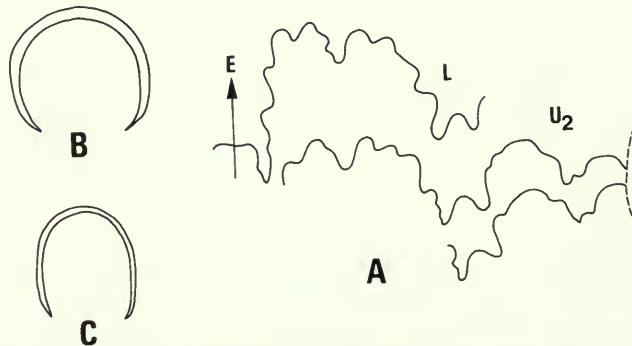


Fig. 47 *Protacanthoceras asgeirri* sp. nov. 47A, sutures, $\times 8.3$, and 47B, whorl section, $\times 2$, of OUM K4433. 47C, whorl section of OUM K4434, $\times 2$.

The paratype is a more robust individual, in which the tuberculate stage is not visible, the outer whorl bearing ribs only. As in the holotype, these are differentiated into flexuous primary ribs with intercalated short ribs. There are *c.* 26 ribs per whorl and three distinct constrictions on the last half whorl. The suture line is very simple (Fig. 47A) with a narrow E, a smaller, asymmetrically bifid L with a few incisions and a smaller U_2 with a single median element. E/L is broad and asymmetrically bifid, U_2 and the auxiliaries on the suspensive lobe are almost ceratitic. This is the simplest suture we have seen in the genus.

DIMENSIONS. Percentage figures in brackets.

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb</i> : <i>Wh</i>	<i>U</i>
OUM K4433	14.1 (100)	5.8 (41)	5.6 (40)	1.04	3.6 (26)
OUM K4434	16.0 (100)	7.2 (45)	6.8 (43)	1.05	3.8 (24)

DISCUSSION. This is the smallest species of *Protacanthoceras* we have seen and the whorl section and the ornament of the early and middle growth stages are so distinctive that it is unlikely to be confused with any other. The ornament of juveniles of *P. tuberculatum* at diameters of 5 mm and less is very like that of the present species at much larger sizes, both showing the distinctive broad distant ribs with rather rounded tubercles, and we would suggest that the diminutive *asgeirri* is a paedomorphic derivative of that species.

OCCURRENCE. The species is only known from Askerswell.

Protacanthoceras bunburianum (Sharpe)
(Figs 29–33, 41–43, 48)

- 1853 *Ammonites bunburianus* Sharpe: 25; pl. 9, figs 3a–c.
 1860 *Ammonites bunburianus* Sharpe; Pictet & Campiche : 315.
 1896 *Ammonites hippocastanus* var. *compressus* Jukes-Browne in Jukes-Browne & Hill : 157; pl. 5, figs 4, 4a only (*non* 1a–b, 3a–b).
 1923 *Protacanthoceras bunburianum* (Sharpe) Spath : 144.
 1923 *Protacanthoceras compressum* (Jukes-Browne) Spath : 144.
 1925 *Ammonites bunburianus* Sharpe; Diener : 24.
 1925 *Acanthoceras hippocastanus* (Sow.) var. *compressa* Jukes-Browne et Hill; Diener : 161.
 1951 *Protacanthoceras bunburianum* (Sharpe); Wright & Wright : 28.
 1951 *Protacanthoceras compressum* (Jukes-Browne); Wright & Wright : 28.
 1957 *Protacanthoceras compressum* (Jukes-Browne); Wright : L414, figs 534, 534a, b.
non 1962 *Protacanthoceras* aff. *compressum* Avnimelech & Shores : 532; pl. 15, figs 2a–b; text-fig. 2 (= *Thomelites* sp.).
 1970 *Protacanthoceras compressum* (Jukes-Browne); Kennedy : 658.
 1970 *Protacanthoceras bunburianum* (Jukes-Browne); Kennedy : 658.
 1970 *Protacanthoceras* spp. Kennedy : 660, 664, 666 (*pars*).
 1971 *Protacanthoceras bunburianum* (Sharpe); Kennedy : 97; pl. 31, figs 1a–c.
 1971 *Protacanthoceras compressum* (Jukes-Browne); Kennedy : 98; pl. 32, figs 2a–d.
 1972 *Protacanthoceras bunburianum* (Sharpe); Thomel : 99.
 1972 *Protacanthoceras compressum* (Jukes-Browne); Thomel : 100.

HOLOTYPE. By monotypy the original specimen figured by Sharpe (1853 : pl. 9, figs 3a–c), BM(NH) 50155. It is said to be from Chardstock but as discussed by Kennedy (1971 : 98) this is, in all probability, an error, for all other known specimens of the species come from the *Calycoceras naviculare* Zone fauna of Division C of the Cenomanian Limestone and its equivalents and are of middle Late Cenomanian age; the phosphatic Basement Bed of the Chalk at Chardstock is of Middle Cenomanian age (Kennedy 1970).

OTHER MATERIAL. Numerous specimens, including the lectotype (GSM 53484, sel. Wright & Wright 1951) of *Protacanthoceras compressum* (Jukes-Browne), from the remanié phosphatic fauna at the base of Division C of the Cenomanian Limestone of the Devon coast between Pinhay Bay and Humble Point : BM(NH) 47736, C8006–7, C73049–50, C73052, C81897, C81963–93; GSM Zn 9082–3, Zn 9085–7; JMH CC328, CC774; OUM K4445–53. From the same horizon

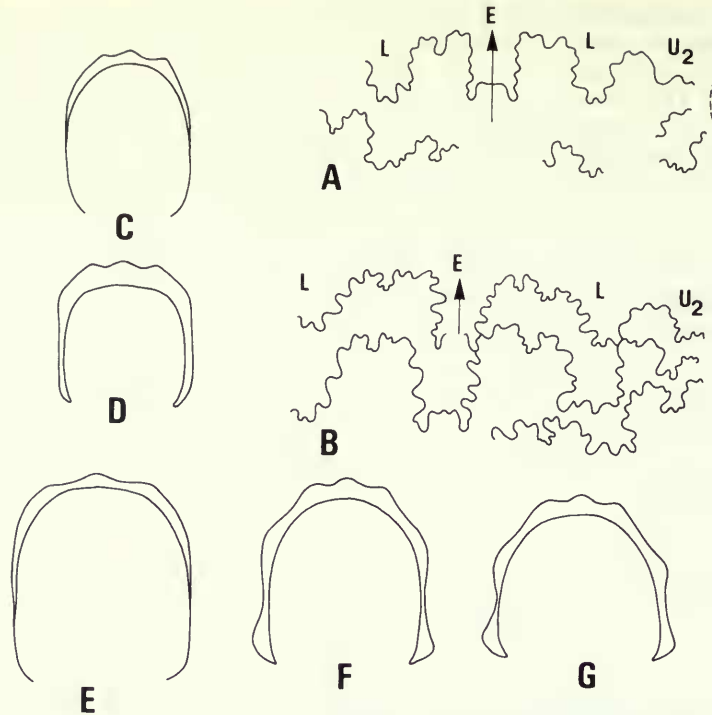


Fig. 48 *Protacanthoceras bunburianum* (Sharpe). 48A, suture of BM(NH) C81968, $\times 4$. 48B, suture of BM(NH) C82001, $\times 4$. 48C, whorl section of BM(NH) C81968, $\times 2$. 48D, whorl section of BM(NH) C81992, $\times 2$. 48E, whorl section of adult body chamber of BM(NH) C81969, $\times 2$. 48F, whorl section of body chamber of BM(NH) C81993, $\times 2$. 48G, section of phragmocone of BM(NH) C81969, $\times 2$.

at the White Hart Sandpit, Wilmington, Devon: BM(NH) C76263, C78575, C81994-7 and OUM K4474-5; 'West of Culverhole', Devon: BM(NH) C73038; 'Landslips at Bindon', Devon: BM(NH) C72983; 'Beer Head': BM(NH) C12591; Hooken Beach, C81998-9; Haven Cliff,

Figs 49-50 *Protacanthoceras proteus proteus* subsp. nov., from the *Calycoceras naviculare* Zone fauna of Bed C of the Cenomanian Limestone, Whitlands, Pinhay Bay, Devon. 49a-b, paratype, BM(NH) C82003. 50a-d, holotype, BM(NH) C82002.

Fig. 51a-d *Protacanthoceras proteus baylissi* subsp. nov. Holotype, BM(NH) C81300 (ex O. H. Bayliss coll. no. OB 268), from the *Calycoceras naviculare* Zone fauna of Bed C of the Cenomanian Limestone at Shapwick Grange, Devon.

Fig. 52a-b *Protacanthoceras tuberculatum devonense* subsp. nov. A paratype, BM(NH) C81953, from the *Calycoceras naviculare* Zone fauna of Bed C of the Cenomanian Limestone at White Hart sandpit, Wilmington, Devon.

Fig. 53a-b *Protacanthoceras* sp. nov. (?) of Matsumoto, Saito & Fukada (1957: 39; pl. 14, fig. 3) from the Trigonina Sandstone (Middle Cenomanian) of Katsurazawa, Ikushumbets, Hokkaido, Japan.

Fig. 54a-d *Protacanthoceras imperatoris* sp. nov. Holotype, from Ankomaka, Madagascar, and in the late General M. Collignon's collection.

Fig. 55a-b *Acanthoceras* aff. *cuspidum* Stephenson. BM(NH) C82005, from the *Calycoceras naviculare* Zone fauna of Division C of the Cenomanian Limestone of Whitlands, Pinhay Bay, Devon.

Fig. 56a-b *Acanthoceras cuspidum* Stephenson. Paratype, USNM 105975, from the Templeton Member of the Woodbine Formation, gullies just south of the Old Sherman Highway, 2.8 miles E of Whitsboro, Grayson County, Texas, U.S.A.

All figures are $\times 1.125$.



49a

49b

51a

51b

51c

51d



50a

50b

50c

50d

52a

52b



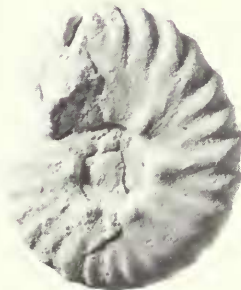
53a



54a



54b



54c



54d



53b



55a



55b



56a



56b

Seaton, BM(NH) C82000-1; also numerous specimens from Shapwick Grange, in the O. H. Bayliss collection.

DIAGNOSIS. Compressed, flat-sided, with 16-28 ribs per whorl, mostly long and bearing umbilical bullae and rounded inner ventrolateral tubercles. Outer ventrolateral and siphonal tubercles are clavate and closely spaced.

DESCRIPTION. The holotype of *Protacanthoceras bunburianum* is a well-preserved phosphatic internal mould of which just over half the last whorl is body chamber. The whorl section is compressed, the breadth to height ratio ($Wb : Wh$) being 0.74, with the greatest breadth below mid-flank; the coiling is involute, with half the previous whorl covered.

The whorl sides are flat, parallel, with a broadly rounded ventrolateral shoulder and narrow, arched venter, rounder between the ribs, but angular in costal section. The umbilicus is small (8% of diameter), shallow, with a low wall and broadly rounded shoulder.

There are 27-28 ribs on the outer whorl. On the phragmocone these are broad and flat and separated by narrow interspaces. All ribs are long, every other rib bearing a faint umbilical bulla. There is a faint swelling at the inner lateral position and a delicate outer ventrolateral and siphonal clavus. On the body chamber the ribs become markedly broader and flatter across the ventrolateral shoulder, with a gently inclined back and steep front slope. Towards the aperture transverse striae appear on all ribs, the umbilical bullae disappear and the ventral tubercles become weaker.

The suture is of standard *Protacanthoceras* pattern, with plump and little-divided elements.

DIMENSIONS. Percentage figures in brackets.

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb : Wh</i>	<i>U</i>	Ribs per whorl
a. Macroconchs						
Holotype, BM(NH) 50155	32.8 (100)	11.0 (33)	14.8 (45)	0.74	8.0 (24)	27-28
BM(NH) C81969	32.0 (100)	9.8 (31)	11.0 (34)	0.89	11.4 (35)	18-19
BM(NH) C81974	29.2 (100)	11.0 (37)	11.9 (41)	0.92	8.6 (29)	—
BM(NH) C81967	24.8 (100)	8.2 (33)	9.5 (38)	0.86	6.4 (26)	23
b. Microconchs						
BM(NH) C81992	18.3 (100)	7.8 (42)	7.4 (40)	1.05	4.3 (23)	19
BM(NH) C81999	21.7 (100)	7.2 (33)	8	—	—	18
BM(NH) C82001	22.4 (100)	8.6 (38)	7.5 (33)	1.14	—	16
BM(NH) C81968	22.5 (100)	7.0 (31)	8.8 (39)	0.79	5.5 (24)	20

DISCUSSION. The examination of large collections of *Protacanthoceras* from Division C of the Cenomanian Limestone on the Devon coast has convinced us that there is every gradation between the feebly ornamented holotype of *Protacanthoceras bunburianum* and the robustly ornamented lectotype of *P. compressum*, and that the two specimens represent the extremes of variation within one species. There also emerge strong indications of dimorphism, with macroconchs generally mature at diameters ranging from 26 to 33 mm and with 18 to 28 ribs on the outer whorl and microconchs mature between 17 and 22 mm and generally with 16 to 20 ribs on the outer whorl. The types of both *bunburianum* and *compressum* are macroconchs, and as can be seen from a comparison of Figs 29-33, 41-43, the range of variation is similar in both macroconchs and microconchs.

P. bunburianum is readily distinguished from all its contemporaries. The closest similarities are between microconchs of *bunburianum* and macroconchs of *P. tuberculatum devonense* subsp. nov. (p. 76). These latter are, however, invariably more coarsely and sparsely ribbed and tuberculate, with a much more depressed whorl section. Rare compressed individuals of *Protacanthoceras tuberculatum tuberculatum* also resemble this species.

OCCURRENCE. *Protacanthoceras bunburianum* is one of the commonest ammonites in the remanié phosphatic *Calycoceras naviculare* Zone fauna of Division C of the Cenomanian Limestone on the south Devon coast and its equivalents inland at Beer, Wilmington and Furley.

Protacanthoceras proteus sp. nov.

TYPES. The **holotype** is BM(NH) C82002, and there are two paratypes, C82003 and C82004, all from the remanié phosphatic fauna at the base of Division C of the Cenomanian Limestone, fallen blocks near Whitlands, Humble Point, Charton Bay, between Lyme Regis and Axmouth, Devon (high *Calycoceras naviculare* Zone).

NAME. After the sea god Proteus, who could assume many different forms, in allusion to the distinctive forms taken up by the species at various stages in ontogeny.

DIAGNOSIS. Depressed, round-whorled with strong umbilical bullae giving rise to pairs of flexuous ribs; conical inner ventrolateral and clavate outer ventrolateral and siphonal tubercles variably developed, effaced during later growth.

Protacanthoceras proteus proteus subsp. nov.

(Figs 49–50, 57)

TYPES. As above.

DIAGNOSIS. Depressed, round-whorled with strong umbilical bullae giving rise to pairs of flexuous ribs bearing distinct conical inner ventrolateral tubercles, and clavate outer ventrolateral siphonal tubercles. Occasional ribs are intercalated. The clavate ventral tuberculation declines on the body chamber.

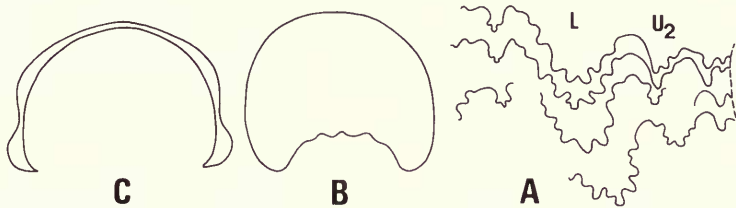


Fig. 57 *Protacanthoceras proteus proteus* subsp. nov., based on the holotype, BM(NH) C82002. 57A, suture, $\times 4$. 57B, whorl section at back of body chamber, $\times 2$. 57C, whorl section at aperture, $\times 2$.

DESCRIPTION. The holotype is a phosphatic internal mould of an adult. About three-fifths of the outer whorl are body chamber and the last few sutures are approximated.

The coiling is moderately involute, with just less than half the previous whorl covered. The umbilicus is moderately broad (25% increasing to 28% at the largest diameter) and deep. The umbilical seam is crenulate to accommodate the ventrolateral tubercles of the preceding whorl. The umbilical wall is low and abruptly rounded. The whorl section is slightly depressed in intercostal section, with gently inflated convergent flanks and an evenly rounded venter. The costal proportions give a much greater whorl breadth to height ratio, 1.67 at the umbilical bulla on the early body chamber and 1.20 closer to the aperture where this bulla is lost. The greatest breadth is at the bulla, where present.

The visible parts of the phragmocone are ornamented by strong, pointed umbilical tubercles, 7–8 to a whorl, which arise from broad low ribs on the umbilical wall. From the bullae there generally arise two well-marked but low rounded ribs, which flex slightly across the flanks and carry small, sharp inner ventrolateral tubercles which become stronger as size increases. From these tubercles the ribs project strongly forwards and become stronger across the shoulder, to join small, delicate, clavate outer ventrolateral tubercles, linked by a very subdued rib to somewhat stronger clavate siphonal tubercles. Occasional intercalated ribs arise low on the flank and sometimes connect to an umbilical bulla on the opposed flank; these bear inner and outer ventrolateral and siphonal tubercles. On the body chamber the ornament changes quite markedly. Siphonal and outer ventrolateral clavi disappear, although up to the aperture their site is marked by distinct spiral striations. The inner ventrolateral tubercles strengthen over the rear part of the body chamber, but decline towards the aperture. The ventral ribbing, weak on the phragmocone,

increases markedly as tuberculation declines and is strongly projected into a broad linguiform sinus. On the flanks the umbilical bullae strengthen markedly and then disappear suddenly, leaving the last three ribs arising well up the flank and virtually lacking tubercles. The ventral parts of the aperture are thus markedly constricted compared to the same region of the shell in middle growth. The sutures (Fig. 57A) are only incompletely visible but are relatively little incised. E is not discernible; L is shallow and broadly V-shaped, with rounded, finger-like incisions, U_2 shallow and little-divided. E/L is broad and bifid with a shallow median incision. L/ U_2 is very simple and almost ceratitic, whilst there is a series of simple, entire frills on the suspensive lobe.

DIMENSIONS. Percentage figures in brackets.

	D	Wb	Wh	Wb : Wh	U
Holotype, BM(NH) C82002 at:	20.7 (100)	8.9 (43)	7.4 (36)	1.20	5.8 (28)
at:	16.4 (100)	10.53 (64)	6.3 (38)	1.67	4.1 (25)

DISCUSSION. The larger paratype has stronger ornament on the body chamber (Fig. 49) but of the same style as that of the holotype; the smaller paratype is slender but has identical ventral tuberculation on the outer whorl and ribs and clavate tubercles similar to those of the holotype on the phragmocone.

Only two other species have comparable overall form. Of these *P. tegulicium* sp. nov. (p. 88, Fig. 44) differs in lacking the clavate ventral tuberculation and branching of ribs and in having more strongly imbricate ribs on the body chamber. There are, naturally, close similarities to *P. proteus baylissi* subsp. nov. (Fig. 51) which we separate on the basis of less pronounced umbilical tuberculation, much straighter ribs and indistinct ventral tuberculation (although the smaller paratype has a marked inner ventrolateral angulation). It is clear, however, that the two are intimately related.

The most interesting feature of *P. proteus proteus* is without doubt the striking similarity of the general proportions and style of ornament, in some respects, to the earliest *Vascoceras*, *V. diartianum* (d'Orbigny). Although *Vascoceras* lacks all but umbilical tubercles, the similarities of the body chamber of *P. p. proteus* to the whole shell of *diartianum* may be significant for the evolutionary origins of *Vascoceras*.

OCCURRENCE. As for holotype.

Protacanthoceras proteus baylissi subsp. nov.
(Figs 51, 58)

HOLOTYPE. BM(NH) C81300, formerly Col. O. H. Bayliss' coll. no. OB 268, from the remanié phosphatic fauna at the base of Division C of the Cenomanian Limestone, high *Calycoceras naviculare* Zone, Shapwick Grange, Devon. BM(NH) C81301 (OB 266), from the same horizon and locality as the holotype, may also belong to this species.

NAME. After Col. O. H. Bayliss, of Spring House, Uplyme, Dorset, who collected the type specimen.

DIAGNOSIS. A depressed, inflated *Protacanthoceras* with rounded whorls ornamented by seven conical umbilical bullae which give rise to groups of 2–3 strong, rounded, recti- to prorsiradiate and more or less straight ribs, with no ventral tuberculation on the outer whorls.

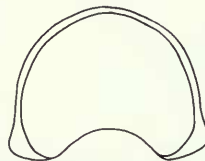


Fig. 58 *Protacanthoceras proteus baylissi* subsp. nov. Whorl section of holotype, BM(NH) C81300 (OB 268), $\times 4$.

DESCRIPTION. The holotype is a phosphatic internal mould retaining approximately half a whorl of body chamber; it appears to be adult.

The coiling is moderately involute during most of development but the adult body chamber uncoils somewhat, giving a lesser degree of involution (Fig. 51a, c). The umbilicus is of moderate breadth and depth (25% of diameter at 20 mm; 24% of diameter at 18 mm). The whorl section (Fig. 58) is depressed and reniform, with an intercostal whorl breadth to height ratio ($Wb : Wh$) of 1.25 and the greatest width low on the flanks. The costal whorl section gives an even higher ratio of 1.42, the greatest breadth being at the umbilical bullae.

The umbilical wall is rounded, with seven low, broad ribs arising at the umbilical seam. These strengthen into strong conical to radially elongate bullae at the umbilical shoulder, strength of bullae increasing towards the aperture. Groups of 2–3 ribs are tenuously linked to these bullae and are weak and low on the flank although becoming stronger across the ventrolateral shoulder and venter. The ribs are rounded, narrower than the interspaces and recti- to somewhat prorsiradiate; they vary from straight to slightly concave aperturally and pass gently forwards across the ventrolateral shoulder to be only weakly projected into a very broad and shallow convex ventral sinus. There are perhaps 22 such ribs on the outer whorl, suggesting the presence of rare intercalated ribs. Apart from the umbilical bullae there is no other obvious sign of tuberculation, although the definite strengthening of the ribs on the ventrolateral shoulder may indicate the presence of a tubercle in this position on the inner whorls. In one instance a rib does not complete the loop from flank to flank but dies out on the venter (Fig. 51d).

Occasional interspaces (generally between two ribs groups) are a little more marked than others but scarcely merit the name constriction.

The suture cannot be fully resolved, but consists of very simple, little-divided elements, with rounded, finger-like incisions on both lobes and saddles.

DIMENSIONS. Percentage figures in brackets.

	D	Wb	Wh	$Wb : Wh$	U
Holotype, BM(NH) C81300	20.5 (100)	—	7.9 (39)	—	5.1 (25)
at: 18.4 (100)	11.1 (60)	7.8 (42)	1.42	4.5 (24)	

DISCUSSION. The second specimen tentatively referred to *P. proteus baylissi* is a juvenile; it shows traces of inner and outer ventrolateral tubercles. *P. proteus baylissi* most closely resembles the contemporary *P. proteus proteus*, from which it is readily distinguished by lack of strong inner ventrolateral tubercles on the whole of the outer whorl and a lack of delicate clavate outer ventrolateral and siphonal tubercles on the septate parts of the outer whorl. The ribbing style is also different, being concave and projected across the ventrolateral shoulders in *proteus* but much straighter in *baylissi*.

As in the case of *P. p. proteus*, *P. p. baylissi* shows interesting resemblances to the early whorls of certain early Turonian vascoceratids. Whereas *P. p. proteus* may foreshadow *Vascoceras*, *P. p. baylissi* shows some resemblance to juveniles of species of *Fagesia* such as *F. harmanni* Böse; the generic transformation would have involved complete loss of ventral tuberculation, increasing depression of whorls, strengthening of bullae and increase in depth of constrictions (incipient in *P. p. baylissi*) to the prominence they take on in *Fagesia* (Powell 1963 : pl. 34, figs 2–5; Pervinquierè 1907 : pl. 20, figs 2a–b, 3a–b, 5a–b).

OCCURRENCE. As for holotype.

Protacanthoceras imperatoris sp. nov.

(Figs 54, 59D)

?1937 *Protacanthoceras tropicum* Stol.; Collignon : 63; pl. 1, figs 1, 1a, 1b.

1964 *Protacanthoceras tropicum* Stol.; Collignon : 146; pl. 373, fig. 1623.

HOLOTYPE. Collignon's (1964) figured specimen from the Cenomanian of Ankomaka, Madagascar; Collignon collection.

NAME. Latin *imperator*, general; in reference to the late General M. Collignon of Moirans, Isère, who collected the type specimen and who helped and encouraged us in many ways.

OTHER MATERIAL. Two specimens from Anabatsifaka, Madagascar, described by Collignon in 1937, may also belong to this species, although we have not examined the original material.

DIAGNOSIS. Compressed, round-whorled with 7–8 conical umbilical bullae giving rise to single flexuous ribs with 2–3 ribs intercalated, showing an early decline of lower ventrolateral tubercles and a body chamber on which all tuberculation but the umbilical is lost.

DESCRIPTION. The coiling is rather involute on the early whorls, although the umbilical seam egresses towards the aperture on the last whorl, with the umbilicus of moderate size.

The umbilicus is shallow, with a low rounded wall and an abruptly rounded umbilical shoulder. The whorls are compressed, the flanks flattened and subparallel, with a rounded venter in intercostal section, the greatest breadth being low on the flanks. The greatest breadth in intercostal section is at the umbilical bulla, where present, with a breadth to height ratio ($Wb : Wh$) of 0.83.

There are 7–8 well-defined, conical to comma-shaped umbilical bullae per whorl. These give rise to single ribs, with one or two other ribs more tenuously connected by mere striae. The ribs are quite low, rounded and crowded, gently flexed and slightly prorsiradiate. There are small, conical inner ventrolateral tubercles at the smallest diameter visible, but these are rapidly effaced, although their position is marked by a broadening, strengthening and projection of the rib, which passes across the venter with a slight broadening at clavate outer ventrolateral and siphonal tubercles, which decline over the later parts of the body chamber. One or two ribs are intercalated between the long ribs, arising on the lower or middle flank, to give a total of *c.* 28 ribs on the outer whorl.

Body chamber modifications, indicating the specimens to be adult, include a weakening of the flank ribs, a disappearance of the umbilical bullae and projection of the ribs on the venter into distinct chevrons.

The last few sutures of the holotype are approximated and rather simple.

DIMENSIONS. Percentage figures in brackets.

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb : Wh</i>	<i>U</i>
Anabatsifaka specimen (after Collignon)	17.0 (100)	9.0 (53)	8.0 (47)	1.13	5.0 (29)
Holotype	24.1 (100)	7.8 (32)	9.3 (39)	0.83	7.2 (30)

DISCUSSION. The holotype was originally referred to '*Protacanthoceras*' *tropicum* (Stoliczka), which we believe to be a juvenile *Thomelites* (p. 101). The holotype of *tropicum* retains siphonal tubercles to a much greater size than *P. imperatoris* and lacks the obviously mature body chamber ornament; these alone suffice to differentiate the two species. Differences from *P. bunburianum* are also obvious and include much stronger clavate ventral tuberculation and a higher, compressed whorl section in the latter. Perhaps the closest species is *Protacanthoceras involutum* Thomel (1972 : 100; pl. 32, figs 5–8) from the Cenomanian of Peille, Alpes-Maritimes, the dimensions of whose holotype and only known specimen are as follows (after Thomel):

<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb : Wh</i>	<i>U</i>
26.4 (100)	80 (30)	12.5 (47)	0.64	5.6 (21)

The specimen is a little distorted by compaction but shows the following features which distinguish it from *P. imperatoris*: strong inner ventrolateral tubercles, retention of all tubercles to a later stage in development and a stronger projection of ribs across the ventrolateral shoulder.

OCCURRENCE. The holotype is said to be from Collignon's Middle Cenomanian Zone of *Euomphaloceras euomphalum*, but the same locality has yielded *Pseudocalycoceras harpax* (Stoliczka) and varieties, *Lotzeites aberrans madagascariensis* Collignon, *Calycoceras cottreaui* Collignon, *Eucalycoceras spathi* Collignon and other species suggesting rather an Upper Cenomanian horizon.

Other species previously referred to *Protacanthoceras*'*Acanthoceras*' *cuspidum* Stephenson
(Figs 56, 59C)1952 *Acanthoceras cuspidum* Stephenson : 203; pl. 50, figs 1-4.1971 *Protacanthoceras cuspidum* (Stephenson) Kennedy : 122.

TYPES. The holotype, by original designation, is USNM 105974, from the Templeton Member of the Woodbine Formation, gullies south of the old Sherman Road, 2·8 miles east of Whitsboro, Grayson County, Texas. Two paratypes, USNM 18971, from the same horizon and locality as the holotype, and USNM 14092, from the Templeton Member of the Woodbine Formation, bluff south of the Missouri-Kansas-Texas Railroad, 1 mile north and 1·85 miles east of Sadler, Grayson County, Texas.

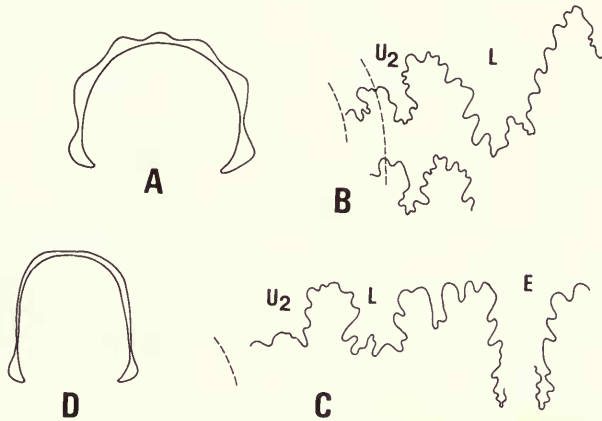


Fig. 59 59A-B, *Acanthoceras* aff. *cuspidum* Stephenson, BM(NH) C82005. 59A, whorl section, $\times 2$. 59B, partial sutures, $\times 4$. 59C, *Acanthoceras cuspidum* Stephenson, suture of USNM 105974, $\times 4$. 59D, *Protacanthoceras imperatoris* sp. nov. Whorl section of holotype, $\times 2$.

DISCUSSION. Stephenson's *Acanthoceras cuspidum* closely resembles strongly-ribbed and tuberculate variants of *Protacanthoceras bunburianum* and also some variants of *P. tuberculatum*. For these reasons we had been inclined to regard the species as a North American example of the genus. Examination of the type specimens has shown that the similarity of ornament is superficial only. They show no signs of reaching or even approaching maturity, whilst the sutures (Fig. 59C) are distinct from those of any *Protacanthoceras* we have seen. These features indicate that *cuspidum* is a juvenile of some other genus.

There are some comparisons to be made with the genus *Dunveganoceras* Warren & Stelck (1940); particularly striking is the asymmetry of the outer ventrolateral clavi in profile, with steep front and gently inclined back faces, whilst there are basic sutural similarities (Cobban 1953 : pl. 10, figs 1-6). We would suggest that '*Mammites*' *bellsanus* Stephenson (1952 : 202; pl. 50, figs 1-4), which also comes from the Templeton Member, may be a *Dunveganoceras*, which lends some support to the placement of *cuspidum* in that genus.

OCCURRENCE. The species is only known from the type occurrence in Texas. It is extremely difficult to place this stratigraphically in terms of the north-west European sequence, but the Templeton Member is certainly older than the *gracile* Zone. The occurrence of a *Eucalycoceras* of the *pentagonum* (Jukes-Browne) group (USGS collns, Denver, ex J. P. Conlin coll.) in the Templeton Member, and the rare occurrence of *Metengonoceras dumbli* (Cragin) in the Upper Cenomanian of Sarthe provide evidence that the unit is approximately equivalent to the *naviculare* Zone and of middle late Cenomanian age. The occurrence of a specimen in Division C of the Cenomanian Limestone, described below as '*Acanthoceras*' aff. *cuspidum*, lends support to this view.

'*Acanthoceras*' aff. *cuspidum* Stephenson
(Figs 55, 59A, B)

compare: 1952 *Acanthoceras cuspidum* Stephenson : 203; pl. 50, figs 1-4.

MATERIAL. One specimen only, BM(NH) C82005, from the high *Calycoceras naviculare* Zone remanié phosphatic fauna at the base of Division C of the Cenomanian Limestone, Pinhay Bay, Devon.

DESCRIPTION. The specimen is a glauconitized phosphatic internal mould, with most of the ventral region of the outer whorl lacking. The last third of the outer whorl is body chamber and the last few septa are neither crowded, approximated nor simplified, indicating the specimen to be immature.

The coiling is very evolute, less than a quarter of the previous whorl being covered, the lower ventrolateral tubercles of which are exposed in the umbilicus. The umbilicus is quite large (34% of diameter) and relatively deep, with a high, vertical, rounded wall and abruptly rounded shoulder. The umbilical seam is crenulated to accommodate the tubercles of the previous whorl. The whorl section is depressed, with flattened, gently rounded flanks, a rounded ventrolateral shoulder and venter, the whorl breadth to height ratio being 1.22, and the greatest breadth at a point below mid-flank. The costal section is polygonal, the greatest breadth being at the umbilical bullae, with a breadth to height ratio of 1.30. There are ten umbilical bullae which vary greatly in strength, from mere swellings at the juncture of two ribs to prominent conical protruberences. They give rise to pairs of ribs (or rarely a single one), which are generally broad, prors- or rectiradial and straight, and which in turn bear strong conical to subspinose inner ventrolateral tubercles.

The ventral ornament is highly distinctive, a low broad swelling crossing the venter bearing very strong, sharp, elongate outer ventrolateral and siphonal clavi. The siphonal row are longer than the ventrolateral and all clavi have a striking asymmetry in profile with a very steep adoral face.

There are only *c.* 16 ribs on the outer whorl.

The suture (Fig. 59B) is incompletely visible, but appears to have been relatively little subdivided. L/U₂ is markedly asymmetric; U₂ is small and rather narrow, whilst the largest of the auxiliaries is also asymmetric.

DIMENSIONS. Percentage figures in brackets; the maximum diameter of the specimen is 28 mm.

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb</i> : <i>Wh</i>	<i>U</i>
BM(NH) C82005 costal	21.1 (100)	10.5 (50)	8.1 (38)	1.30	7.2 (34)
intercostal	21.1 (100)	9.3 (44)	7.6 (36)	1.22	7.2 (34)

DISCUSSION. The affinities of this specimen are somewhat cryptic. The sparse ribbing and coarse ornament recall the *Protacanthoceras tuberculatum* group (Figs 14-17) and, to a degree, the contemporary *P. tuberculatum cyclopeum* (Fig. 45). None of these, however, shows the same style of ventral ornament with elongate clavi, and this alone serves to distinguish the specimen from that species. This ornament and the asymmetric profile of the clavi strongly recall the coarsely ornamented variants of *P. bunburianum*, but none of these show the depressed whorl section, strong spinose umbilical and ventrolateral bullae nor the same retention of ornament. In these respects the specimen more closely resembles the North American '*Acanthoceras*' *cuspidum* Stephenson (Fig. 56); even here there are differences, however, for *cuspidum* has denser, more crowded ribs and bullae, stronger lower ventrolateral tubercles which are produced into spines (possibly a reflection of the presence of shell material) and an umbilicus in which the lower ventrolateral spines are visible on the wall of the succeeding whorl (although again this may be a reflection of the presence of shell material in the American specimens). There are also obvious differences in the suture (compare Figs 59B and C) such as to preclude reference to '*Acanthoceras*' *cuspidum* itself.

OCCURRENCE. As for figured specimen.

Ammonites tropicus Stoliczka

(Figs 4-5, 60A-D)

- 1865 *Ammonites tropicus* Stoliczka : 78; pl. 43, figs 2, 2a, 2b.
 1898 *Acanthoceras tropicum* (Stoliczka) Kossmat : 122.
 1925 *Acanthoceras tropicum* (Stoliczka); Diener : 166.
 non 1937 *Protacanthoceras tropicum* (Stoliczka); Collignon : 63; pl. 1, figs 1, 1a, 1b.
 non 1964 *Protacanthoceras tropicum* (Stoliczka); Collignon : 146; pl. 373, fig. 1623.
 1972 *Protacanthoceras tropicum* (Stoliczka); Thomel : 99.

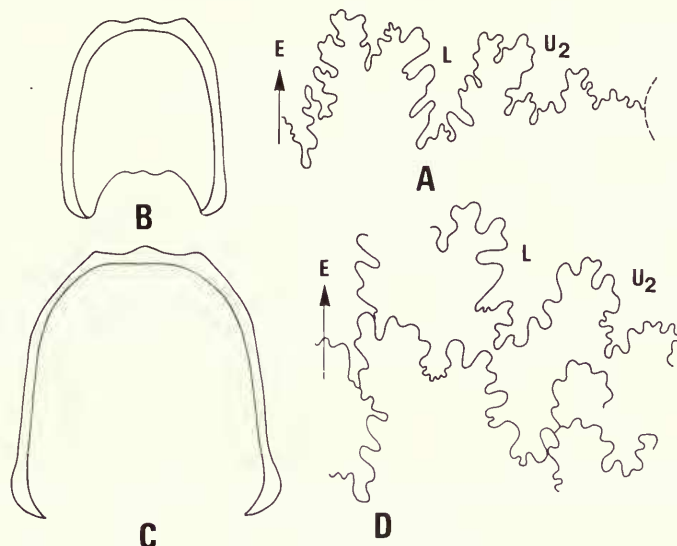


Fig. 60 *Ammonites tropicus* Stoliczka. 60A, suture, $\times 4$, and 60B, whorl section, $\times 2$, of the holotype, after Kossmat. 60C, whorl section, $\times 2$, and 60D, suture, $\times 4$, of BM(NH) C12590.

HOLOTYPE. By monotypy Stoliczka's original specimen from the Utatur Group, north of Odium, southern India.

DISCUSSION. Most authors since Spath's introduction of *Protacanthoceras* have referred *Ammonites tropicus* to this genus and indeed Stoliczka noted how similar his species was to Sharpe's *Ammonites bunburianus*. As the original figures show (Fig. 5a-b), however, the holotype retains all its tubercles to the aperture and at a diameter of 27 mm is still immature. Furthermore the suture (reproduced here as Fig. 60A) has deeply incised and subdivided elements quite distinct from the very simple sutures of typical *Protacanthoceras*, a deep E, a smaller but narrow L and a relatively broad U_2 , E/L bifid and deeply incised, L/ U_2 small and bifid, with one large and several smaller, poorly-defined auxiliaries on the suspensive lobe.

Other specimens referred to the species (Collignon 1937, 1964) are quite distinctive and have been described above as a new species, *Protacanthoceras imperatoris* (p. 97).

The affinities of *Ammonites tropicus* are much closer to *Thomelites* and we figure here (Fig. 4a-c) a juvenile from the Upper Cenomanian of southern England which is closely related to, if not conspecific with, Stoliczka's species.

Ammonites triserialis J. de C. Sowerby

- 1836 *Ammonites triserialis* J. de C. Sowerby in Fitton : 239, 344; pl. 18, fig. 27.
 1863 *Ammonites triserialis* Sowerby; Pictet : 39.
 1923 *Protacanthoceras triserialis* (J. de C. Sowerby) Spath : 144.
 1925 *Acanthoceras triserialis* (Sowerby in Fitton) Diener : 166.
 1951 *Protacanthoceras triseriale* (J. de C. Sowerby); Wright & Wright : 29.

1971 *Protacanthoceras triseriale* (J. de C. Sowerby); Kennedy : 99.

1972 *Protacanthoceras triseriale* (Sowerby); Thomel : 99.

DISCUSSION. The name *Ammonites triserialis* was introduced by J. de C. Sowerby in the description of fossils illustrated by Fitton, who (1836 : 239) lists '*A. triserialis* Pl. XVIII, f. 27. Mr. Sowerby's Museum', in a 'List of Fossils from the sands of Blackdown and of some other places in Devonshire'. In his explanation he points out that all the fossils in his list are from 'the Whetstone Pits at Blackdown, except those to which a different locality is assigned'. He thus lists a variety of fossils from other localities and indeed horizons, such as *Ammonites hippocastanus* and *varians* from Pinhay. Sowerby's specimen has disappeared but, on the basis of the figure, Spath (1923 : 144) regarded the species as an early *Protacanthoceras* which gave rise to *P. compressum* (Jukes-Browne) and *P. bunburianum* (Sharpe), apparently believing it to be related to the rather depressed, square-whorled *Protacanthoceras* of the *tuberculatum* group from the Middle Cenomanian Chalk Basement Beds of south-west England. Following Spath we both initially suggested (Wright & Wright 1951; Kennedy 1971) that the species was a *Protacanthoceras* and inferred that it came from a Basement Bed of the chalk of south-west England.

Sowerby's specimen bears no resemblance to any of the species here included in *Protacanthoceras*. But for the clear statement in Fitton (1836: table on p. 366) that it came from Blackdown and the unlikelihood of Sowerby or Fitton confusing a phosphatic specimen from the Devon coast with the siliceous preservation for which Blackdown was famous, we should have had no hesitation in treating it as a *Calycocheras* (*Newboldiceris*) from the Cenomanian Bed C of the coast sections. It bears an extremely close resemblance to one of the characteristic 'post-spinosum' forms from that horizon, although in the absence of the specimen there must remain slight doubt as to its identity.

***Protacanthoceras* sp. nov. (?) of Matsumoto, Saito & Fukada**
(Figs 53a-b)

1957 *Protacanthoceras* sp. nov. (?); Matsumoto, Saito & Fukada : 39; pl. 14, fig. 3.

MATERIAL. The original figured specimen, no. GH 7874, in the collections of Hokkaido University, from the Middle Cenomanian *Trigonia* Sandstone of Katsurazawa, Ikushumbets Valley, Hokkaido (*ex* Nemoto collection).

DISCUSSION. This tiny specimen is immature and bears weak, irregular flank-ribs, rounded inner ventrolateral tubercles and clavate outer ventrolateral tubercles which are stronger than the siphonal row. In our view it is not possible to place it generically with any confidence; it may be a juvenile *Acanthoceras*, or even a *Protacanthoceras* juvenile comparable to the *tuberculatum* group rather than to *P. compressum* (i.e. *bunburianum*) with which Matsumoto, Saito & Fukada compared it.

OCCURRENCE. Middle Cenomanian of Hokkaido, Japan.

Discussion: Evolutionary trends

Most of the material described in this paper comes from diachronous, condensed phosphatic Chalk Basement Beds, the fossils in which are known to have complex histories (Kennedy & Garrison 1975). In spite of this, the various associations of species can be fitted into the biostratigraphic sequence determined in the expanded chalk sequence of south-eastern England and northern France (Kennedy 1969; Juignet & Kennedy 1976) and the broad outline of evolution of *Protacanthoceras* is clear. Within this framework inferences about the relationships of species which occur in the same Basement Bed in the same area have been made on morphological criteria, with, in some cases, clues from differential preservation (e.g. differing numbers of phases of mineralization). Subject to these limitations the evolution of *Protacanthoceras* can be seen as follows (Fig. 61).

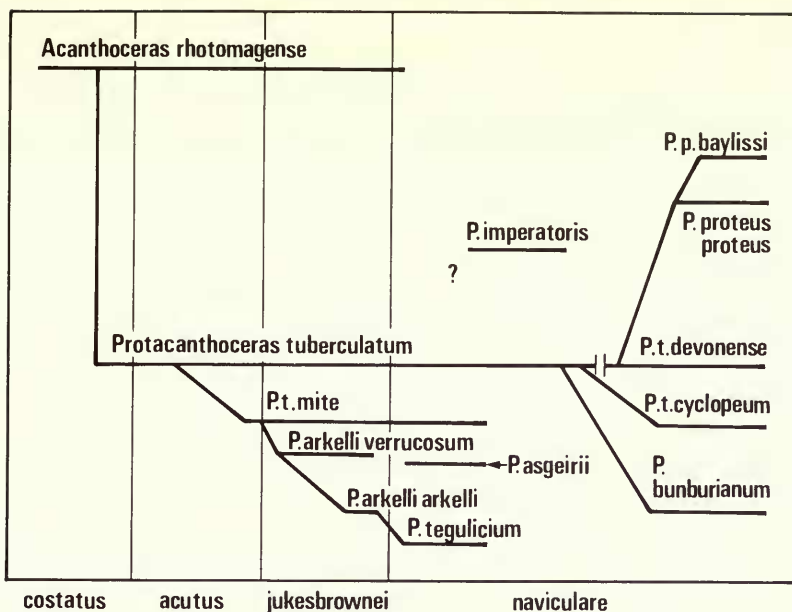


Fig. 61 The phylogeny of *Protacanthoceras* species.

The genus is a pedomorphic derivative of *Acanthoceras rhotomagense*, appearing for the first time in the early Middle Cenomanian. The rootstock of the genus is *Protacanthoceras tuberculatum* Thomel, the nominate subspecies of which survived until the mid Upper Cenomanian. During late Middle Cenomanian time a slender, feebly-ornamented subspecies, *P. tuberculatum mite*, evolved and gave rise to the compressed, weakly-ornamented subspecies, *P. arkelli*, which shows very striking ontogenetic changes, involving loss of all ventral ornament in middle growth. Rare examples of an intermediate form, *P. arkelli verrucosum*, are known. The nuclei of *P. arkelli* are constricted and lack siphonal and outer ventrolateral tubercles, being miniatures of the early Upper Cenomanian *Protacanthoceras tegulicium*, which is interpreted as a pedomorphic derivative of *arkelli*. The innermost whorls of early Upper Cenomanian *P. tuberculatum* are also a miniature of the middle growth stage of the diminutive *P. asgeirri*, which is likewise regarded as a pedomorphic offshoot of the *tuberculatum* stock.

The latest *Protacanthoceras*, from the mid Upper Cenomanian, probably derive from the *tuberculatum* group. *Protacanthoceras tuberculatum cyclopeum*, the largest form, is the product of evolutionary size increase, whilst typical *P. tuberculatum devonense* is a product of evolutionary size decrease. Both have essentially the same style of ornament as *P. tuberculatum tuberculatum*.

Some variants of *P. tuberculatum devonense* show a weakening of ventral tuberculation and a rounding of the whorls, which strongly suggests that this subspecies is the origin of *Protacanthoceras proteus proteus* and *P. p. baylissi*.

P. bunburianum, type species of the genus, stands separated from its contemporaries by a clear morphological hiatus, but rare compressed late Middle Cenomanian *Protacanthoceras* of the *tuberculatum* group may be close to its ancestral stock.

Protacanthoceras imperatoris cannot be related to any of the stages in the evolutionary sequence described above. This species and a series of interesting *Protacanthoceras*-like micromorphs from the Cenomanian of the U.S. western Interior, kindly shown to us by Dr W. A. Cobban, may even be quite independent offshoots of *Acanthoceras* species other than *rhotomagense*, filling the same ecological niche as the European species of *Protacanthoceras* in the Malagasy and U.S. Interior ammonite faunas.

There is a striking resemblance between *Protacanthoceras* and several other genera, although there is insufficient evidence to confirm the relationships suggested below beyond doubt, whilst

there is always a tendency to regard any genus studied in depth as the key to the phylogeny of the higher taxonomic group to which it belongs.

Thomelites, which first appears in the early Upper Cenomanian, has many *Protacanthoceras*-like features, especially in tuberculation and rib style, although the sutures (Fig. 23E, p. 81) are more complex than in *Protacanthoceras*. The early, multi-tuberculate stage of Lower Turonian *Nigericeras* (Fig. 10a–b) are similar to the early developmental stages of *Protacanthoceras asgeirri*, magnified several times, although no intermediates are known from the *Sciponoceras gracile* Zone faunas which separate them.

The flank ribbing, body chamber ornament and suture of *Protacanthoceras p. proteus* closely resemble those of the earliest *Vascoceras*, *V. (Vascoceras) diartianum* (d'Orbigny), from the succeeding late Cenomanian *Sciponoceras gracile* Zone. Similarly, *P. proteus baylissi*, which is ribbed and bullate and has virtually lost its ventral tubercles, resembles juvenile *Fagesia* in many respects, although it is less markedly depressed and constricted.

Finally, compressed variants of *Protacanthoceras bunburianum* show strong resemblance to *Quitmaniceras brandi*, of Lower Turonian age, which has a tuberculate siphonal keel.

These similarities between the various Upper Cenomanian *Protacanthoceras* fauna and later acanthoceratids are of great interest, but it is unlikely we have found the missing links between Cenomanian and Turonian acanthoceratid faunas.

Our study of *Protacanthoceras* provides good examples of paedomorphosis as an important mechanism in ammonite evolution. The record, restricted admittedly by the nature of the available collections, appears to show speciation in this genus in part as a series of sudden jumps in morphology, that is saltation, and in part, in the case of the *tuberculatum* rootstock, as a clear example of gradual change.

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Index

New taxonomic names and the page numbers of the principal references are in **bold** type. An asterisk (*) denotes a figure.

- Acanthoceras* 66–7, 69, 71, 74, 102–3
bassae 67
cuspidum 99*
jukesbrowni 71, 74, 78, 82, 86
rhotomagense 65–7, 69–70, 77*, 81*, 103
confusum 66
sussexiense 66
tropicum 101
'Acanthoceras' cuspidum 71, 93*, 99–100, 99*
 aff. *cuspidum* 100
 Acanthocerataceae, Acanthoceratidae, Acanthoceratinae 68–104
Acompsoceras 66
landesi 66
sarthense 66
 Algerian Sahara 71
Ammonites bunburianus 68, 91, 101
hippocastanus 102
 var. *compressus* 76, 91
triserialis 101–2
tropicus 71, 77*, 101
varians 102
 Askerswell 67, 72, 74, 76, 78, 82, 86, 88, 90–1
 Axmouth 95
 Beachy Head 72
 Beer 94
 Bindon Slips 67, 92
 Blackdown 102
 Burham 72
Calycoceras 66, 69–70
cottreai 98
(Gentoniceras) gentoni 77*
naviculare 70, 72, 74, 76, 78, 80–2, 86, 88, 90–2, 94–6, 100
 Cenomanian 65, 68–9, 72, 74, 97; see Middle, Upper Cenomanian
 Limestone 66, 72, 74, 76, 78, 80–2, 86, 91–2, 94–6, 99–100
 Chaldon 71
 Chalk Basement Bed 66, 68, 71–2, 74, 76, 78, 82, 86, 88, 90–1, 102
 Chard 68–9, 76, 78, 86
 Chardstock 67, 82, 91
 Charton Bay 95
 Chilfrome Lane 67
Conlinoceras 70
 Dallas 81
 Devon 66–8, 70–1, 76, 78, 80–2, 86, 92, 94, 96, 100, 102
 Dorset 66–8, 70–1, 74, 76, 78, 82, 86, 88, 90
Dunveganoceras 71, 99
 Durdle Cove 67, 72
 England 66, 70, 102
Eucalycoceras 99
spathi 98
Euomphaloceras euomphalum 98
 Evershot 68, 71
Fagesia 97
harmanni 97
 Fort Worth 81
 France 66, 69, 71, 76, 81, 102
 Furley 68, 72, 94
Gentoniceras, see *Calycoceras*
 Glynde 72
 Grayson County 92, 99
 Haven Cliff 92
 Hokkaido 81, 92, 102
 Hooken Beach 68, 76, 86, 92
 Hooken Cliff 68
 Horn Hill 68, 71
 Humble Point 68, 76, 81–2, 86, 91, 95
Hyphoplites 66
 India 76, 101
 Japan 71, 92
 Jurassic 67
 Kent 70, 72

- Lotzeites aberrans madagascariensis* 98
 Lower Turonian 76, 104
 Lulworth Cove 68, 74, 78
 Lyme Regis 95
- Madagascar 66, 69, 71, 76, 92, 97–8, 103
 Maiden Newton 67, 71
 Malagasy 103
 ‘*Mammites*’ *bellsanus* 99
 Man-of-War Cove 68, 72
 Mantelliceratinae 66
Metengonoceras dumbli 99
Metioceras 70
 geslinianum 81
 latoventer 70
 praecox 70
 Middle Cenomanian 66–7, 69–70, 72, 74, 78,
 91–2, 98, 102–3
- Neocardioceras* 70
Newboldiceras 70, 102
 Nigeria 76
Nigericeras 70, 104
 costatum 70, 77*
 Normandy 70
- Odium 76, 101
 Osmington 68, 71, 74, 78
- Paracompsoceras* 66
 Peille 71, 96
Peltoceras 89
 Pindiga 76
 Pinhay Bay 86, 91–2, 100, 102
Protacanthoceras 65–7, 68–104
 arkelli 66, 76, 82–8, 85*, 89, 103
 arkelli 83*, 84–6, 85, 103
 verrucosum 76, 83*, 85*, 86–8, 103
 asgeirri 70, 79*, 90–1, 90*, 103–4
 bunburianum 66–8, 70, 80, 82, 83*, 87*, 91–5,
 92*, 98–100, 102–4
 compressum 69, 74, 91, 94, 102
 cuspidum 99
 dentonense 70
 hippocastanum 69
 imperatoris 71, 93*, 97–8, 99*, 101, 103
 involutum 98
 proteus 66, 72, 89, 95
 baylissi 66, 80, 82, 87*, 89, 93*, 96–7, 103–4
 proteus 66, 80, 82, 93*, 95–6, 95*, 97, 103–4
 tegulicium 66, 86, 87*, 88–90, 89*, 96, 103
 triserialis, *triseriale* 66, 69, 101
 tropicum 97, 101
 tuberculatum 65–9, 71–82, 78*, 83*, 91, 99–100,
 102–3
 cyclopeum 66, 74, 80–2, 84*, 85*, 100, 103
 devonense 66, 74, 76–80, 87*, 93*, 94, 103
 mite 66, 70, 74–6, 75*, 79*, 103
 tuberculatum 69, 71–4, 72*, 75, 77*, 78*, 79*,
 80, 82, 88, 94, 103
 Provence 71, 74
Pseudocalycoceras 66, 69
 aff. *dentonense* 81
 harpax 69–70, 98
 ankomakaensis 77*
- Quitmaniceras* 70
 brandi 70, 104
 reaseri 70
- Ringstead Quarry 68, 71, 74, 78, 82, 86
 Rouen 70, 74, 86
- Sarthe 70, 76, 81, 99
Sciponoceras gracile 81, 104
 Shapwick Grange 68, 76, 80, 86, 92, 94, 96
 Snowdon Hill 68–9, 71, 76, 78, 86
 Somerset 68–70, 76, 78
 Surrey 74
 Sussex 70, 72
- Templeton Member 92, 99
 Texas 81, 92, 99
Thomelites 67, 69–71, 91, 98, 101, 104
 aff. *sornayi* 77*, 81*
 Tinhaert 71
 Toller Porcorum 68, 71
Trigonia Sandstone 92, 102
 Turonian 66; see Lower Turonian
Turrilites acutus 71, 74, 76, 78, 86
 costatus 70–1, 74, 76, 81
 naviculare 71
- Upper Cenomanian 66, 70–1, 98–9, 103–4
 Upper Cretaceous 67
- Vascoceras* 96–7, 104
 diantianum 96, 104
- White Hart Sandpit 68, 72, 76, 78, 92
 White Nothe 68, 71, 74
 Whitlands 68, 72, 76, 86, 92, 95
 Wilmington 72, 74, 76, 78, 92, 94
 Wiltshire 70, 74